

# 原始观音座莲属 (*Archangiopteris*) 的正誤研究\*

秦仁昌

(中国科学院植物研究所)

最近几个年代里,古生物学的研究,所积累的大量证据已充分揭示了在进化上显然已不再是很活跃的观音座莲目(Marratiales)。这蕨类植物,不仅是现代蕨类植物中最古老的一群植物,并且还证明了观音座莲蕨类型的植物在地球上的存在是漫长而古老的,它的起源和历史发展可以追溯到古生代的上半纪。当时在地球表面上的许多地区(包括向北分布到北纬 $70^{\circ}$ 以北的地区,如格陵兰),已出现了许许多多的现在已成为化石的观音座莲蕨类型的植物(如 *Scolecopteris*, *Asterotheca*)。它们的内部构造和孢子囊群的特征已显示和现代还活着的而仅只分布于北纬 $30^{\circ}$ 以下(如峨眉山)的残遗代表有着极大的相似之点。虽然具有高耸乔木状主干(如星囊蕨, *Asterotheca arborescens* 的主干高达10米以上)和蕨类形叶体、并且生长着和近代观音座莲相同的子囊群的植物,远在中生代后期已被发现,但毕竟一直到了中生代的前半期的地层里,人们才第一次见到了在体形上和子囊群的结构上真正近似于近代型的这群植物,而这群植物的最繁荣时期却开始于石炭纪的末期,经过侏罗纪一直到白垩纪的整个漫长的时期里,它们曾代表着广泛分布的三十个以上的属,并且是当时地球上植被组成的优势分子。实际上,近代观音座莲目是整个近代蕨类植物门中的唯一的植物群,它在亲缘关系上能和许多最古老的化石植物具体的联系起来,可以清楚的看出它们之间在演化上的来龙去脉。

从古代很长一个时期里,在种属数量的繁多上和分布的广泛性上,曾经盛极一时的观音座莲蕨类植物群中到今日还存在的子遗植物只有六个属,代表大约三百多个种。它们广泛分布在地球上的热带和亚热带地区,如多孔蕨属或称单蕨属(*Danaea*)分布于南美洲;合囊蕨属(*Marrattia*)分布于东西两半球;观音座莲属(*Angiopteris*)分布于东半球,向北展延到亚洲大陆的东南和西南部;大叶观音座莲属(*Macroglossum*)与天星蕨属(*Christensenia*)只分布于马来群岛的个别地区,并且后者向北延展到亚洲大陆的热带边缘,而有趣的原始观音座莲属(*Archangiopteris*)按它的现时分布,却是云南东南部——东京地区特有的蕨属,向东经广西南部伸展至海南岛和台湾,还未发现于其他任何地区。如已被知道的那样,在系统发育上,这群古老的植物在近代蕨类植物的很长以来的进化过程中,显然已不再参加什么活动了,而它们近代的子遗种几乎还停留在和它们祖先的同一进化水平上。因此,它们在近代蕨类植物中除掉瓶尔小草目(*Ophioglossales*)外,实在还找不到和它

\* 本文在1957年5月举行的中国科学院第二次学部大会生物学部宣读。

們在古老性上相同的伙伴了。瓶尔小草目的植物,虽然从它的内部解剖和子囊羣的形态特性看,也是代表着极其古老的植物羣,很可能还要老过观音座蓮蕨羣,但到现在为止,却还没有在古生代的地层里找到它的祖先的遺骸——化石,因此还不能判定它的起源的绝对地质年代。

观音座蓮目的六个属中,有三个属产于中国热带及亚热带地区。其中观音座蓮和原始观音座蓮这两个属很早以前就知道了;而第三个属叫天星蕨属(*Christensenia*)在中国的发现只是两年以前的事,也是在云南东南部被发现的,它的代表种叫做 *Christensenia assamica* (Griff.) Ching, (新組合),原产印度北部,它和馬來亞地区产的 *C. aescurifolia* (Bl.) Maxon 是不大相同的,虽然过去是被认为同一种的。

在简单地介绍了整个观音座蓮目的一般历史起源和地理分布之后,讓我們轉移到本文的主题——原始观音座蓮的討論。在此以前,对它的形态特征,系統分类和地理分布等方面还是了解得不多的,茲扼要分述如次:

## 一、历史起源

根据已知的化石材料,現在似乎可以比較肯定的說,原始观音座蓮的历史起源可以追溯到石炭紀时代的一些植物,特别是 *Danaeopsis fecunda* Halle 可以說是本属的原始型。因为从它的羽片形体和子囊羣的結構看,都显得同原始观音座蓮相同,虽然它的主脉間的小脉是网状型的,这可能是叶片加寬的結果。

在系統发育上,原始观音座蓮被認為是古老的观音座蓮目的进化系列上的最高的一支,它和观音座蓮的关系最为密切,前者可以被認為是后者的直属后代,但由于通过了漫长的历史演化过程,获得了自己特有的一系列的特征,形成了厚囊蕨类在进化路綫上一个最新的里程碑。

## 二、地理分布

在地理分布上。原始观音座蓮自成一个小区域,大約位于北緯 19—24°30' 与东經

106—122° 之間的一條东西走向的狭长热带和亚热带季雨常綠林的地帶,在这里的湿润山地原始森林里也还茂盛地生长着观音座蓮属的許多种,并且在这里也第一次发现了同羣的天星蕨属(*Christensenia*)。从現在已知的种的分布来看,可以说云南东南部——北越这个地区是原始观音座蓮蕨的发源地和分布中心,向东經广西南部展伸至海南島及台湾。近年来的研究指出,云南东南部从它整个植物区系发展史來說,已有許多例証可

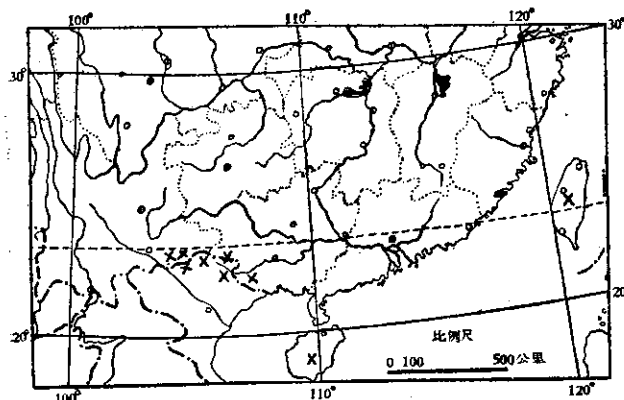


图1 原始观音座蓮屬的地理分布

Fig. 1 A map showing geographical distribution of *Archangiopteris Christ et Gies*.

以說明本区是許多比較古老的殘遺植物种属的分布中心或发源地。这些古热带植物区系自第三紀以来在比較稳定——特别是未遭到冰川的侵袭的气候条件和相当复杂的地形变化下,形成了一个自然避难所,使这些种类不仅保存下来而且有些还可能繼續获得发展。原始观音座蓮就是古代殘遺植物区系的一分子在这个地区里发展起来的一个例子(參閱图 1)。

### 三、形态特性

原始观音座蓮属是瑞士蕨类学家 Christ 和 Giesenhagen 二氏于 1899 年根据英国 Augustine Henry 氏在云南东南部的蒙自区采得的标本而建立的,曾被認為是个单种属。它的发现曾經引起了世界植物系統分类学家和形态解剖学家的极大兴趣,但由于缺乏新鮮材料,在解剖方面至今还没有很好地加以研究。在它被发现后的二十余年中,在毗邻云南的越北地区又发现了二种,1919 年又在台湾也发现一种,1935 年又在越北发现一种,至 1935 年止共有五种。但在过去的二十余年中,通过中国植物学家們自己的活动,从他們所采集的材料中,經過研究,又发现了五种,都产于云南东南部的湿润山地常綠闊叶季雨林中。

在这里要說明的主要的并不在于发现了新种的数目,而在于由于这些发现和进一步研究了过去已知的种类的结果,揭露了一些在形态上的新的特征,使我們对这一羣从远古殘遺下来的植物的許多方面获得了比較全面的認識。总结起来,有如下几点:

(1) 从来学者們認為,作为原始观音座蓮的形态特征之一,是这羣植物的叶体总是“一回羽状”的,在有关文献里都是把这一点作为区别于有“二回羽状复叶”的观音座蓮属的特征之一的,但随着一种二回羽叶种 (*A. bipinnata* Ching) 在云南东南部的被发现,这个特征已經不再是原始观音座蓮的一个重要的了,虽然一回羽叶仍然是它的一般形态通性。

(2) 从来学者們認為原始观音座蓮的細长綫形子囊羣下面一般具有夹絲,叫做“睫毛状的鱗片”或者“假子囊羣盖”,現在从所有已知种的研究,証实了夹絲并不是一种什么鱗片,而實質上就是毛,形态上叫做夹絲。它們在子囊羣下面的存在不只是个經常的属的特性,而且这些由柱状或棒状的多細胞組成的节状淡棕色的毛并不是单毛(有时有腺状的头),而毫无例外地都是分枝状的毛。至于毛的长短乃和不同的种类有一定关系的,在大多数的种,夹絲的长度是等于或稍长过于孢子囊的高度,但在另两个种,它們的夹絲則远比孢子囊为短,隐藏于孢子囊羣的下面,因此,从孢子囊羣上面观察,却看不到它們的存在;在另一个种 (*A. hokouensis* Ching),它的夹絲由多达 15 个柱状細胞組成,要比子囊大約长过二倍,而且多而密生,使发育着的孢子囊羣好象要从絨毛茸中钻出来似的。

(3) 在原始观音座蓮的所有种的叶柄上,如同南美洲产的多孔蕨属 (*Danaea*) 一样,大約在它中部以下的部位,生有一个有沟槽的肉質节状隆起,但有趣的是,在一个新发现的种 (*A. hokouensis* Ching),它的叶柄上却具有 4—5 个同样的节状隆起,排列于整个叶柄的各部,因此,看起来好象竹桿一样。可以指出,近代观音座蓮蕨目在它們叶柄上的这种不平凡的节状隆起,对于生物体有着相当重要的生理上的意义的,因为这种内部充滿液汁的节状隆起,証明是生物体在生理过程中,用来調节叶面对于阳光的方向和強度(即空气

湿度的变化)的一种有效机制,根据需要或不需要,用来控制整个叶体下垂或是上升运动云。

(4) 众所周知,原始观音座莲属,得以区别于观音座莲属的另一个特征是它的由 40—60—160 个孢子囊组成的长綫形孢子囊羣,而在新发现的一种里 (*A. hokouensis* Ching) 却有由多达 240 个孢子囊组成的长达 3.5 厘米的孢子囊羣,而在另一个新种里即 *A. bipinnata* Ching, 孢子囊羣一般只由 20 个孢子囊组成,也有更少的,这都是过去未曾见过的现象。

(5) 在原始观音座莲属的种类里,过去不知道有所谓“逆行假小脉”的存在,即在两条真脉中间从叶边出现向中肋方向倒行的一根“假脉”,这种现象在观音座莲属的许多种是相当普遍的。但在越北发现的一种原始观音座莲 (*A. Cadieri* Tard. et C. Chr.) 的各对真脉中间竟然同样出现一条“逆行假小脉”的存在。不但如此,它的较短的 (35—50 个孢子囊组成) 孢子囊羣的位置也和其他的种类有所不同,它不是生于叶边与中肋之间,而是生于靠近叶边,好象观音座莲属的种一样。由于这个种的发现,更足以证明原始观音座莲这属植物是直接起源于观音座莲属的,而不应该认为是一个趋同现象。应该指出,由于这些证据和其他形态特点的不同 (如鳞片的形成,腹背状的根茎等等),正如上面已经指出那样,原始观音座莲在它被发现的当时,Christ 和 Giesenhagen 两氏认为是代表极原始的蕨类植物,因而叫它为 *Archangiopteris*, 而现在从形态发生的研究,知道这个名词的含义是很不妥当的,因为它在历史演化的阶段上并不比观音座莲属更古老、更原始。相反的,应该是后来的或是派生的一支。

由于以上一系列的新特征的发现,原始观音座莲和观音座莲这两属的概念,在许多方面起了一些重大的变化,甚至有些过去被认为的区别,如果不认为已经站不住的话,现在至少已经大大的削弱了。虽然如此,由于许多新特征的发现,这两个亲缘相近的属之间的区别仍然是真实的,不可混淆的。因此,关于原始观音座莲属的界说概念应有重新厘定的必要,同时关于两个属的区别,也有重新划分的必要。

虽然我们承认了原始观音座莲属在亲缘关系上最接近于观音座莲属,但它具有如下一些形态上的基本特征:

- (1) 整个形体较小,较简化和较细弱。
- (2) 根茎颇细长,斜出,为腹背型。
- (3) 总叶柄细弱,肉质,基部具一对肉质的大椭圆形的宿存托叶,至少具一个,有时多至五个沟槽状的肉质节状膨大,干则变为扁压而黑色。
- (4) 鳞片相当发达,尤以叶柄下部为多,披针状,具粗筛孔,基部卵圆形,深心脏形,腹部着生。
- (5) 叶一般为一回奇数羽叶,少为二回羽叶,羽片大而少数,通常 1—5 对,闊披针形,小叶柄膨大,干则变为黑色。
- (6) 子囊羣长,一般由 40—240 个分离的孢子囊组成,不为叶边着生,而却着生于中肋与叶边之间的中部,下部有很多分枝的节状多细胞夹丝衬托。
- (7) 孢子具有微细刺状密生的外孢壁。



## 四、系統分類

### 原始观音座蓮屬

**Archangiopteris** Christ et Gies. in Flora 86: 72—85, 1899.

本属为中型陸生蕨類植物，生于热带山地常綠闊叶林中，根狀莖頗長，亚直立或斜生，有腹背之分和肥粗肉質不分枝的長根疏生；叶簇生，通常 3—4 成丛，柄長，頗細，肉草質，上面有一寬縱溝槽，近基部处有不少長綫形暗棕色具粗篩孔的鱗片，腹部着生，邊緣有粗齿牙，向上部疏生或几光滑，基部有一对頗大的薄肉質卵狀長圓宿存的托叶狀的附屬物包围，向中部有一个(有时 4—5 个)肉質节狀膨大，上面有縱溝，干后成扁压，呈淡黑色；叶片卵形到卵狀三角形，比叶柄为短，照例为一回奇数羽狀，少有二回羽狀，羽片一般为 1—6 对，互生或亚对生，闊披針形，漸尖头，有小柄，頂生一枚羽片同側生的同形而通常較大，小柄也膨大，干后也变淡黑色；叶脉分离，从中肋向外斜向上开展，一次分叉或为单脉，明显，直达叶边，多少向上弯弓，頂端尖削，不具倒行假脉 (*A. Cadieri* 除外)，草質或紙質，綠色，上面光滑，下面通常鱗片疏生；孢子囊羣为長綫形，沿叶脉中部着生，照例位于邊緣与中肋之間，但既不达中肋也不达叶边，每羣由 20—60—160—240 个，船形的无柄分离的成两排紧靠的孢子囊組成，孢子囊的頂部有不发育的胚帶并以腹部的一縱縫开裂，放出大量孢子，下面有沿叶脉着生的夹絲，夹絲的長短不一，节狀，腺头，透明，分离，干后易擦落；孢子略圓或闊卵圓形，乳黃色，透明，表面有短細刺头密生的外孢壁。

本属为一个很自然的属，現有 10 种，产云南东南部及越北，向东分布到广西南部，海南及台湾。

毫无疑問，本属同观音座蓮属有着密切的亲緣关系，其不同之点为植株形体較小，較簡單和較細瘦，根狀莖頗長，亚直立，有腹背之分，細瘦的叶柄基部有两瓣薄肉質卵狀長圓形的托叶，接近中部有一个(有时更多的)有沟槽的肉質节狀膨大，叶柄下部有狹長形具粗篩孔的鱗片，边有粗齿牙，腹部着生，叶片远較小而簡單，通常为一回奇数羽狀，只有不多几对远較大的有小柄的羽片，孢子囊羣远較細長，由更多的(一般 40—240 个)孢子囊組成，生于中肋与叶边之間，下面有节狀分枝的夹絲密生和有密細刺头的孢子。

自从 1899 年 Christ 和 Giesenhagen 两氏根据在云南东南部(大围山)的标本，发现了原始观音座蓮属以后，日本植物学家早田文藏(Hayata)氏曾将本属的界說大大地攪乱了一番，他在不到十年的時間内，根据越北及台湾标本，連續发表了两个新属，即 *Protomarrattia* 和 *Protangiopteris*。当他发表 *Protangiopteris* 属时，他显然对原始观音座蓮属的特征的認識是极为模糊的，于是提出了他認為是他的新属的三个特点，就是叶柄中部以下有一个节狀膨大，羽片的小柄不膨大(?)，和孢子囊羣下面有作为假孢子囊羣盖的“鱗片”。但我們現在知道，这三个特征也正是原始观音座蓮属所以区别于观音座蓮属的一些主要特征，因此他的新属必須被認為是原始观音座蓮属的同义名詞。

早田文藏氏的第二个新属 *Protomarrattia* 也是同样不能成立的，虽然曾被 Bower 氏(The Ferns, Vol. II. P. 127)当作一个有效的属看待的。这个属是根据越北的标本建立的，而它的孢子囊羣还在幼年发育阶段，經過干制过程，被压挤得很紧，看起来好像是 *Marrattia* 的合生孢子囊羣那样，除此以外，本属的模式种，*Protomarrattia tonkinensis* Hayata

与产于同地的 *Archangiopteris tamdaoensis* Hayata 并无不同之点,这早已在 1935 年被 Christensen 和 Tardieu-Blot 两氏指出了 (Lecomte, Not. Syst. 5 卷, 3 頁)。

正如 Bower 氏所評述的那样, *Archangiopteris*, *Protomarrattia* 和 *Protangiopteris* 这三个属名的含义是十分令人迷惑的。在它們的創立人的心目中认为这些属在进化上比观音座蓮属 (*Angiopteris*) 和 *Marrattia* 属更为原始,但是这些所謂原始蕨属在孢子囊羣的位置上比之更古老的蕨属离叶边更远处向下延伸,而且叶柄及其他部分只有鳞片而无毛——这两点在蕨类植物一般被认为是原始性的一些指标。如果同地质年代早期的化石——例如上泥盆纪的孢子囊羣为边生蓮座形的 *Coenopteridaceae* 相比,可以証明这些属显然不是比观音座蓮属更为古老,而却由观音座蓮属演化而来的。

长期以来,学者們关于观音座蓮目 (*Marratiales*) 这羣古老的蕨类究竟是代表一个单系羣的科 (*Marratiaceae*), 还是应该分立为几个科或者几个亚科的意见,一直是分歧的。Christensen 氏在 1938 年第一次提出了——我认为这是恰当的——把这个目分为两个科,即观音座蓮科 (*Angiopteridaceae*), 包括 *Macroglossum* Copel., *Angiopteris* 和 *Archangiopteris* 三个属,和 *Marratiaceae* 科,包括 *Marrattia*, *Danaea*, 和 *Christensenia* 三个属,他这样做的主要理由是前一科的孢子囊羣是由分离的并且頂部具有不发育的胚带的孢子囊組成的,而后一科的孢子囊羣則由合生的頂端不具不发育的胚带的孢子囊組成的聚合孢子囊羣。与此相反, Copeland 氏 1947 年在蕨綱植物科属志一书中认为 Christensen 氏的做法在系統发育上是沒足够理由能保証的,但奇怪的是他把本目分立为四个亚科,即 *Angiopterideae*, *Marratieae*, *Kaulfussieae* 和 *Danaeae*。这种安排实际上同現有的证据是不相符合的。

早在 1940 年我曾确切地提出了把天星蕨属 (*Christensenia*) 分立成为一个单独的科,天星蕨科 (*Christenseniaceae*)。这样做的主要理由是它有腹背形的根状莖,掌状叶和网状脉以及圓形的聚合而中空孢子囊羣不具夹絲。从个体发育研究的結果也証明这样做是确当的,因天星蕨的孢子世代的第一个幼叶的形体是鐮形,具有网状脉的特点,而观音座蓮, *Danaea* 和 *Marrattia* 三个属的孢子世代的第一个幼叶是扇形,具有标准的二叉分歧的分离脉型,即此一点也可以作为支持天星蕨比其他各属在进化上较为后来的一个証据,与此同时,美国 Campbell 氏 (*Evolution of Land Plants* 第 330 頁) 也不謀而合地建議把天星蕨属分立为独立的科,叫做 *Kaulfussiaceae*。

現在,如过去一样,我仍坚持我的意見,即多孔蕨属 (*Danaea*) 应该同样地从古老的 *Marratiaceae* 科里分立成为独立科, *Danaeaceae* Agardh, 这样就使 *Marratiaceae* 科只剩下合囊蕨属 (*Marrattia*) 一个属,因为这两个科在系統发育上是代表着不同的近代路綫的,虽然它們十分可能是起源于大約同一个地质年代。

总结上面的討論,可以把观音座蓮目分为如下四科:

1. 观音座蓮蕨科 (**Angiopteridaceae** C. Chr.) 包括 *Macroglossum* Copel., *Angiopteris* Hoffm. 和 *Archangiopteris* Christ et Gies., 三个属。
  2. 合囊蕨科 (**Marratiaceae** Kaulf.) 包括 *Marrattia* Swartz 一个属。
  3. 多孔蕨科 (**Danaeaceae** Agardh) 包括 *Danaea* Smith 一个属。
  4. 天星蕨科 (**Christenseniaceae** Ching) 包括 *Christensenia* Maxon 一个属。
- 現在討論一下孢子囊羣的进化問題。今日已知的丰富化石資料似乎指出聚合孢子囊

羣不一定是由那些具有分離孢子囊羣的蕨類演變出來的次生變異現象，如同 Bower 氏所認為的那樣，而正如 Scott 氏 (Study of Fossil Botany I. p. 366. 1921) 所指出那樣，可能起源於地質年代早期的某羣蕨類。這種說法是正符合於實際情況的，因為遠在古生代，具有分離孢子囊的孢子囊羣的蕨類（如 *Scolecopteris*, *Eoangiopteris*）和具有合生孢子囊的不同類型的聚合孢子囊羣的蕨類（如喬木型的 *Ptychocarpus* 和 *Asterotheca*）它們已經被發現同時存在的了。我也不同意 Bower 氏 (The Ferns II. p. 110. 1927) 認為團形類型的聚合孢子囊羣，如同天星蕨那樣，是由綫形類型的聚合孢子囊羣通過分裂過程演變的結果，而恰恰相反，我倒認為孤立的孢子囊羣能通過融合過程轉變為匯合孢子囊羣是蕨類植物在孢子囊羣進化的一般途徑。這種情況在薄囊蕨綱的一些進步的蕨羣特別看得清楚，而孢子囊羣的分裂在這些蕨類與其說成是一般現象則倒不如當作是一個偶然的或者不正常的現象看待。

更有進者，如眾所周知，不同進化羣系的生物有機體的某些器官構造的相同，往往可能是趨同發展的結果，而不一定是系統進化上親緣關係的指標，關於這一點，一般的蕨類植物的一些特徵，就是如此，例如孢子囊羣的形態，囊羣蓋的有無，這些特徵在半世紀以前曾被當時的蕨類植物學家（如英國的 Hooker 和 Baker 氏等）作為蕨類系統分類的基本準繩，而現在則被視為這只不過是次生的而且往往是趨同的結果而已。在這個問題上，天星蕨屬的親緣關係可以追溯至石炭紀的祖先類型，如 *Ptychocarpus* 或是 *Asterotheca*，它們有團形蓮座狀的聚合孢子囊羣，而與近代的合囊蕨屬 (*Marrattia*) 的關係則遠較疏遠，因為不但它的聚合孢子囊羣是綫形，而且還有許多其他重要形態上的區別。

### 原始觀音座蓮屬的種之檢索表

1. 葉下部為二回羽狀，羽片 10—12 對，長 15 厘米，寬 2.5 厘米，邊緣有齒牙…………… 1. 二回原始觀音座蓮 *A. bipinnata*
1. 葉全部為一回羽狀，有較大和較少的 (1—7 對) 羽片。
  2. 羽片有逆行假小脈自葉邊向下倒行，位於真脈之間；孢子囊羣短 (5—6 毫米) 接近於葉邊，因此，中肋兩側的不育空間遠比近葉邊的為寬…………… 2. 邊囊原始觀音座蓮 *A. Cadieri*
  2. 羽片不具逆行假小脈；孢子囊羣遠較長，位於邊葉與中肋之間，因此中肋兩側的不育空間幾乎等於近葉邊的。
    3. 葉柄基部以上有 4—5 個肉質節狀突起，羽片下面被適度的節狀毛；孢子囊羣長 3—3.5 厘米，有茸毛狀的夾絲密生…………… 3. 河口原始觀音座蓮 *A. hokouensis*
    3. 葉柄只有一個肉質節狀突起，位於中央以下，羽片下面無毛或者不具前種那樣的毛，孢子囊羣一般遠較短，夾絲通常短而較疏。
      4. 側生羽片鐮狀綫披針形，基部一對比上面一對長約一半，基部均為闊圓形或者亞圓形，葉邊全緣…………… 4. 圓基原始觀音座蓮 *A. subrotundata*
      4. 側生羽片通常為披針形，基部一對長等於或者僅稍短於上面一對，向楔形基部漸變狹。
        5. 羽片對生或者亞對生，葉邊有粗齒牙狀的鋸齒；夾絲比孢子囊羣短並且被復蓋不見。
          6. 羽片為闊倒披針形，有尾狀頭，葉邊自基部向上有齒牙；夾絲極短…………… 5. 尾尖原始觀音座蓮 *A. caudata*
          6. 羽片卵狀披針形，有漸尖頭，葉邊自基部向上有弧曲尖鋸齒；夾絲較長…………… 6. 尖葉原始觀音座蓮 *A. tonkinensis*

5. 羽片互生,叶边为全缘,至多为波状,或为圆齿形浅波状;夹丝与孢子囊等长或较长。
6. 羽片为阔卵状披针形,短渐尖头……………7. 阔叶原始观音座莲 *A. latipinna*
6. 羽片为披针形或倒披针形,缓渐尖头。
7. 羽片披针形,平坦,全缘或齿牙形波状,草质,产云南东南部及越北。
8. 羽片 2—4 对,有缓渐尖头,基部对称;孢子囊羣长 1—2 厘米……………8. 亨利原始观音座莲 *A. Henryi*
8. 羽片 5—7 对,急尾尖头,基部不对称;孢子囊羣长 1 厘米……………9. 斜基原始观音座莲 *A. subintegra*
7. 羽片狭倒披针形,叶边波形圆齿状,浅波状,厚纸质,产台湾……………10. 台湾原始观音座莲 *A. Somai*

## 1. 二回原始观音座莲 [图版四十九, 1]

*Archangiopteris bipinnata* Ching, Ic. Fil. Sin. 5: t. 203. 1958.

叶柄长 60—70 厘米,直径约 4 毫米,腹面有深沟,淡绿色,草质,下部略有紧贴的暗棕色披针形长尖头的鳞片,基部以上约 20—34 厘米处有一个膨大的节,叶体三角状卵圆形,长 40—50 厘米,中部宽约 22 厘米,基部为二回羽状,向上为一回奇数羽状;叶片 10—12 对,基部一对或二对羽片特大,长 16—19 厘米,宽 6—7 厘米,有 2.5—3 厘米长的小叶柄,羽裂为 2—7 对侧生小羽片,阔披针形,渐尖,几无柄,开展,并有粗齿牙,长 2—3 厘米,基部以上宽约 1 厘米,圆楔形,顶端小羽片大形,长 7—10 厘米,宽 2.8 厘米;上面的一回羽片有叶柄(长 4—6 毫米),线状披针形,向顶端渐狭为渐尖头,长 12—17 厘米,近中部宽 2—2.8 厘米,基部圆楔形,叶缘全部具有规则的粗齿牙;叶轴干后压扁,向上端两边有狭翅;顶生羽片与相邻的同形;叶为草质,干后为绿色,除叶轴、中肋下面及叶柄膨大处有一些棕色小鳞片外,全为光滑;叶脉上下两面明显,脉间距离 2 毫米,一般为单脉或分叉,几乎成直角从中肋伸出,直行,达于边缘的每一齿牙;子囊羣线形,生于上部一回羽片上的,长约 5 毫米,由近中肋向外伸展到距叶缘 4 毫米处,沿生单脉上或分叉脉上,由 20—40 个孢子囊组成,在孢子囊羣下面有许多密生分枝的夹丝,长等于或稍过于孢子囊,生于小羽片上的子囊羣较短,由 10—12 个孢子囊组成,从小中肋出发几达边缘;孢子暗色,透明,圆而有棱角,表面有粗疣状突起。

产地: 云南东南部, 马关县, 金口(老君山), 馮国楮 13679, 1947 年 11 月 7 日, 生杂木林下, 少见, 海拔 1,100—1,300 米。

本种为本属中最特殊的种,一般体形酷似观音座莲;在原始观音座莲属中发现二回羽叶的种是有很大意义的,因为由这一种的发现,在一定程度上改变了过去对属的界说,打破了过去总是认为一回羽叶为本属的特征之一的传统看法。

## 2. 边囊原始观音座莲

*Archangiopteris Cadieri* Tard. et C. Chr. in Lecomte, Not. Syst. 5: 8. t. 1. fig. 1—2. 1936; in Fl. Gen. Indo-chine 7: 15, 1939.

产安南的 Cua Tung, 海拔 50—100 米的山林。

本种是安南的特有的和特出的种,它不同于本属的其他之种在于如同观音座莲属的一些一样有长约 1 厘米的逆行假小脉一条,位于每对真脉之间,从叶边向下倒行,这个特

征在原始观音座莲属中为前所未見。本种另一特征为其較短的由大約 30—50 个組成的孢子囊羣,向外到达离叶边不远处,向內則止于离中肋很远处,因而在中肋兩側留下很寬的不育空間,这样就使本种在外觀上頗象观音座莲。因此,本种似为在亲緣关系上极相近的原始观音座莲属与观音座莲属之間的中間型。

### 3. 河口原始观音座莲 [图版四十九, 2]

*Archangiopteris hokouensis* Ching, Ic. Fil. Sin. 5: t. 240. 1958.

根状莖粗大,肉質,亚直立,直径 3—4 厘米,下面具鉄絲状的厚肉質的黑色单根;叶簇生,柄长达 50 厘米,厚达 5 毫米,肉質,綠色,有 4—5 个膨大具沟槽而干后为黑色的节状突起,各节間的距离大致相等,另外被有一些卵状披針形而基部为圓心脏形的深棕色鱗片,边緣有长鋸齿;叶体为寬卵形,长达 30 厘米,寬約 38 厘米,一回奇数羽状,頂端小羽片較大,长 20—22 厘米,寬 7—9 厘米;小羽片 2—3 对,同形,对生或亚对生,节距 5—6 厘米,长 15—20 厘米,中部寬 5—7 厘米,闊椭圆披針形,有小柄,長約 1.5 厘米,膨大,淡黑色,略具鱗片,頂部为短尾状漸尖头并具粗鋸齿,向基部漸狹,成楔形,边緣有波状浅齿或波状齿牙;叶为紙質,上面深綠,下面淡綠,并有相当多的节状細毛复盖;叶脉細长頗开展,明显,大都分叉,間为单一,近叶边向上弯弓,并深入鋸齿;子囊羣綫形,长 3—3.5 厘米或較长,彼此頗接近,由 160—240 个子囊成二列組成,不育边緣和中肋兩側寬达 5 毫米,夹絲綫形,稠密,节状分枝,由 10—15 个細胞組成,长过于子囊;孢子短圓形,透明,具密集的小刺状突起。

产地:云南东南部的河口,南溪鎮,朱維明 1726, 1955 年 7 月,生于潮湿浓蔭的林下沟中,拔海 150 米,普通。

本种为本属一个独特的种,其叶柄在基部以上具有 4—5 个节状膨大,小叶很寬,椭圆披針形,边緣有波状鈍鋸齿,下面密生节状毛,子囊羣极长,并具很长的密毛茸状的夹絲,几乎完全复盖着初生的子囊羣。

### 4. 圓基原始观音座莲 [图版五十, 1]

*Archangiopteris subrotundata* Ching, Ic. Fil. Sin. 5: t. 206. 1958.

叶柄长 36—60 厘米,淡綠色,腹面有深沟,有淡紅棕色的綫形鱗片,尤以下部为多,边緣有睫毛,基部以上 20—30 厘米处有膨大的节;叶体长与寬各約 40 厘米,闊卵形,奇数羽状;羽片 4—6 对,頂生羽片与側生的同形,互生,相距約 4 厘米;有小叶柄(柄长 7 毫米,膨大),基部一对甚短,(长 14 厘米),鐮刀状,向上弯弓,与上部的同形,基部圓形,上部羽片长 22—25 厘米,中部寬 5 厘米,闊綫状披針形,漸尖,基部几不变狹,圓形或亚圓形,不呈楔形,叶全緣或至多略呈波状,頂端有鋸齿;叶为薄草質,綠色,除中肋有鱗片疏生外,均为光滑;叶脉开展,明显,相距 4 毫米,单脉或分叉,近边緣显然向上弯弓;孢子囊羣綫形,一般长 8—12 毫米,相距甚远,位于叶緣与中肋之間,两端有等寬的不育空間,有密生分枝的节状夹絲,长过于孢子囊;孢子长圓腎形,有細密刺头突起,透明。

产地:云南东南部,西畴县,馮国楹 12019, 生杂木林下,拔海 1,500—1,600 米。

本种形体頗似亨利原始观音座莲 (*A. Henryi* Christ et Gies), 但羽片不为披針形而为闊平行状披針形,下部的为鐮刀状,基部的羽片远較上部的为短,边緣为全緣,或在頂端以下有时为波状,向圓形或亚圓形的基部不为明显的变狹。

## 5. 尾叶原始观音座莲 [图版五十, 2]

*Archangiopteris caudata* Ching, Ic. Fil. Sin. 5: t. 208. 1958.

根状茎亚直立,粗达2厘米,有粗根,叶柄长30—45厘米,直径3—4毫米,綠色,几无鳞片,在基部以上30厘米处有膨大的节;叶体为卵形,长30厘米,寬約25厘米,奇数羽状;羽片在所見标本为2对,亚对生,相距5—6厘米,頂生羽片稍較大,长16—18厘米,中部寬4.5—5厘米,側生羽片皆为同形或基部一对微較短,闊倒披針形,向楔形的基部漸变狭,頂部突变为尾状(尾头长約1.5厘米,綫形,有锯齿),叶边自基部以上有粗齿牙;叶为草紙質,綠色,上下两面光滑,但沿中肋及叶脉有小披針形鳞片疏生;叶脉亚开展,与中肋成 $60^\circ$ 的上角,大多数分叉,或单脉,近叶緣向上弯弓而达于锯齿;子囊羣长8—10毫米,离中肋及叶边各約6毫米,亚近生,由40—70个子囊組成,少有更多的,托稍隆起,夹絲远較子囊为短,紅棕色,节状,由基部分枝很多;孢子球圓形,具細密刺头,透明。

产地: 广西南部,明江,千牛山,前广西大学生物系采,生半山以上的林内沟中。

本种是一明显的地方种,其不同于亨利原始观音座莲者为其倒披針形的羽片突成尾状头,叶边具粗齿牙,和子囊羣的夹絲非常短,而由基部分枝繁密,不易由上方見到。

## 6. 尖叶原始观音座莲 [图版五十一, 1]

*Archangiopteris tonkinensis* (Hayata) Ching, Ic. Fil. Sin. 5: t. 209. 1958.

叶柄长40—45厘米,淡綠色,腹面有寬沟,有疏生披針形棕色而有齿牙的鳞片,下部較多,基部以上20—30厘米处有膨大的节;叶体闊卵圓形,远短于叶柄,奇数羽状,頂生羽片有长柄,与側生的同形,側生羽片2—4对,对生,斜出或斜开展,卵状披針形,长20—25厘米,寬4—5厘米,有小叶柄(叶柄长約5毫米,膨大,干后近黑色),中部最寬,向两端漸狭,頂端为长漸尖,基部短楔形,叶緣有弧曲形尖锯齿;叶多少为厚堅紙質,腹面光滑,无毛,背面沿中肋有疏生鳞片;叶脉甚开展,很明显,分叉或单脉,向上弯弓,直达锯齿;孢子囊羣长7—10厘米,綫形,位于叶緣与中肋之間,細密而分枝的节状夹絲短于孢子囊,易脫落;孢子长圓形,有微小密刺头突起,透明。

分布: 海南島,越南。

本种頗似亨利原始观音座莲(*A. Henryi* Christ et Gies.),但叶柄远較叶体为长(約两倍),羽片卵状披針形,对生,边緣具有規則的弧曲锯齿,夹絲远短于孢子囊,故易区别。

## 7. 闊叶原始观音座莲 [图版五十一, 2]

*Archangiopteris latipinna* Ching, Ic. Fil. Sin. 5: t. 207. 1958.

叶柄47—55厘米,直径5毫米,腹面有深沟,下部鳞片頗多,基部以上約20厘米处有膨大的节;叶体卵状长圓形,长35—45厘米,寬26—30厘米,奇数羽状;羽片2—3对,互生,相距4—5厘米,斜出,基部一对較短于上部的,鐮刀状向上弯弓,上部羽片长20厘米,寬5—5.5厘米,中部最寬,闊卵状披針形,向下漸狭为楔形基部,頂端为短漸尖或为漸尖头并有锯齿,叶全緣或多少为微波状;小叶柄长1厘米,略为膨大,几无毛;叶为厚紙質,上下两面光滑,惟沿叶軸和中肋下面有一些鳞片;叶脉疏松,开展,单脉或分叉,近叶緣向上弯弓,明显;孢子囊羣长1—1.5厘米,位于叶緣与中肋之間,相距叶緣与中肋各約7毫米,列間有較寬間隙,夹絲密生,略短于孢子囊;孢子亚圓形,有密生微小疣状突起。

产地: 云南东南部,屏边县,蔡希陶 60299,生林下,拔海1,200米。

本种表面上頗似亨利原始观音座蓮 (*A. Henryi* Christ et Gies.), 并曾被認為同种, 但叶为厚紙質, 羽片远較寬, 邊緣呈微波状, 基部一对显然为鐮刀状和子囊羣的間距較寬。

## 8. 亨利原始观音座蓮

*Archangiopteris Henryi* Christ et Gies. in *Flora* 86: 72—85. Fig. 1—5, 1899; Christ in *Bull. Herb. Boiss.* 7: 14. 1899; Hu et Ching, *Ik. Fil. Sin.* 1: t. z. 1930.

根状莖亞直立, 直径 2—3 厘米, 肉質, 有肉質粗健而光滑的长根, 除頂端略有鱗片外, 余均光滑; 叶簇生, 叶柄长 40—60 厘米或較长, 粗約 2.5 毫米, 上面通体有寬沟槽, 綠色草質, 中央稍下处有节状膨大, 有相当多的鱗片, 尤以向基部为甚, 鱗片狹披針形, 长而棕色或深棕色, 質薄, 宿存, 叶体长等于叶柄, 寬約 17 厘米, 卵形, 一回羽状; 羽片 2—4 对, 頂端一枚同形而較大, 有时长达 30 厘米, 寬达 6.5 厘米, 側生羽片互生, 斜出, 彼此分开約 5—6 厘米, 有小柄, 基部一对稍短, 长 12—15 厘米, 寬約 3 厘米, 上面一对长約 17—20 厘米, 中部最寬約 4—5 厘米, 闊披針形, 緩漸尖头, 基部楔形, 向下漸变狹, 小柄长約 1 厘米, 膨大, 有鱗片, 干后变黑色, 叶边全緣或略为波状, 但向頂部有急尖的鋸齿; 叶脉細而疏生, 大約 1 厘米內有 4 条, 极为开展, 两面明显, 大都分叉, 但也往往分叉脉与单脉相間, 向頂部变尖細而向上弯弓, 几达于叶边, 草質, 干后綠色, [两面光滑, 惟叶下面的中肋有棕色狹披針形鱗片疏生; 子囊羣綫形, 通直, 长 10—20 毫米, 被等寬的間隙分开, 由 60—160 个孢子囊羣組成, 位于中肋与叶边之間, 有細而紅褐色的节状分叉夹絲密生, 长过于孢子囊羣。

本种为本属的模式种, 特产云南东南部屏边县, 河口, 麻栗坡山地林下。

本种的主要特点为其披針形的互生的羽片, 向頂端为有鋸齿的緩漸尖头, 向基部为漸狹楔形, 有长約 1 厘米的小柄, 邊緣为全緣或至多有波状齿牙, 孢子囊羣下的夹絲幼时为毛茸密生, 长过于孢子囊。

## 9. 斜基原始观音座蓮

*Archangiopteris subintegra* Hayata in *Bot. Gaz.* 67: 90. fig. 1. 1919.

叶柄长达 70 厘米, 近基部有披針形的基部为圓形的鱗片, 叶体倒卵形, 一回奇数羽状; 羽片 5—7 对, 披針形, 长 20—25 厘米, 寬 3—5 厘米, 向頂部急变为綫形漸尖头, 长約 2—3 厘米, 基部为不等形, 小柄长約 7 毫米, 膨大有鱗片, 叶边亞全緣或波状, 叶質薄; 孢子囊羣长 1 厘米, 位于中肋和叶边之間, 有夹絲疏生, 长过于孢子囊。

本种产于越北的 Chapa 与 Muong Xen 及 Ta Phinh 一带, 靠近云南东南部边境的林下。可能是前种的一个变型。

## 10. 台湾原始观音座蓮 [图版五十二]

*Archangiopteris Somai* Hayata, *Ik. Pl. Form.* 5: 256, 1915; 6: 154, fig. 60 t. 19. 1916; Ching, *Ik. Fil. Sin.* 5: t. 205. 1958.

叶柄长 50—60 厘米, 有疏生鱗片, 尤以下部为多, 基部以上約 25 厘米处有膨大的节; 叶体长卵圓形, 奇数羽状, 羽片 2—3 对, 頂生羽片与下部的同形, 长 20 厘米, 寬 4 厘米, 为微倒披針形, 中部以下漸狹, 基部略为寬楔形, 頂端漸尖, 尾状, 长 3—4 厘米, 互生, 有小叶柄(柄长約 1 厘米), 叶緣浅波状, 基部以上有不規則的圓齿状齿牙; 叶为厚草質或堅紙質, 干后棕色, 几无毛; 叶脉頗开展, 单脉与分叉脉相間; 孢子囊羣綫形, 长 1.5 厘米, 位于中部, 中肋两边及叶緣下面为不育空間, 夹絲短于孢子囊, 隱匿, 从表面不易見到; 孢子圓形

或长圆形, 颇微小, 具疣状突起, 透明无色。

产地: 台湾特产。

本种为台湾南部, 中部及北部高山森林中一种很普通的蕨类, 并与云南东南部的亨利原始观音座莲 (*A. Henryi* Christ et Gies.) 颇相似, 但因羽片为厚草质, 长倒披针形, 有圆齿状齿牙和叶缘为浅波状, 故有不同。

## A REVISION OF THE FERNS GENUS *ARCHANGIOPTERIS* CHRIST & GIESENHAGEN\*

R. C. CHING

(Institute of Botany, Academia Sinica)

(ABSTRACT)

Ample paleontological evidences brought to light within last few decades have revealed in a convincing manner that the group of ferns known as *Marratiales*, though apparently now no longer in a very active state of evolution, is a very primitive group of ferns and that the existence of *Marratiaceus* type of plants is a very ancient one with its origin and historical development dated back to the Upper Palaeozoic Period, at which time a number of fossil forms such as *Scolecopteris*, *Asterotheca*, etc., found in all continents, distributed as far north as 70°N. Lat. show great similarity in regard to anatomical structure and soral character to the living representatives of the group now growing only in regions below 30° N. Lat. (for example, the Mt. Omei in Szechuan Province, West China). Although plants with arborescent stem (up to 10 m high, as *Asterotheca arborescens*) and fern-like fronds bearing sori similar to those of the existing *Marratiaceus* ferns are found as early as in the Upper Palaeozoic flora, it is in the older Mesozoic rocks that we first encounter ferns which agree closely in habit and soral character with the recent representatives of the group. The maximum development of these ferns which seems to have been begun by the end of Carboniferous, extended throughout Permian to Pre-cretaceous time, represented, as is now known, by over 30 extinct genera, which constituted not only widely dispersed but also one of the dominant elements in the vegetation of those times. In fact, the modern *Marratiales* are among the only living ferns which can be definitely associated with the oldest known fossil ancestors.

To-day, of this vast ancient group of plants once of very wide distribution, there remain only 6 pan-tropical genera, assignable, in my opinion, to possibly 4 distinct families (see below) still widely dispersed in the tropics of both hemispheres, namely, *Angiopteris* in the eastern, *Danaea* in the western and *Marrattia* in both, with one Malaysian species (*M. sambucina* Bl.) extending northwards to Cochin-China (Annam), and *Macroglossum* and *Christensenia* in the Malaysian region, the latter extending to the mainland of tropical southeastern Asia, while the interesting genus *Archangiopteris* in its present distribution endemic in a comparatively small area on the Yunnan-Tonkin borderland. This ancient group of plants, as is known to-day, was not directly involved

\*The writer wishes to express his sense of gratitude to Professor W. Y. Chun, the Director of the Institute of Botany, Academia Sinica, Canton, for having been kind enough to read the manuscript in English and make valuable suggestions.



in the evolution of the advanced types of living ferns and its present-day survivors still remain practically at the same stage of evolution as their ancestors of many million years ago. Among extent modern ferns no other group of comparable antiquity exists except *Ophioglossaceae* which though nearly as primitive as *Marratiales*, have not yet been definitely associated with Palaeozoic fossils.

Before we go further in our discussion, it may be well to point out that of the Marratiaceae type of modern ferns only two genera, *Angiopteris* and *Archangiopteris*, had been known to occur in the tropical and subtropical parts of China until 1956, when the discovery of *Christensenia* in the southeastern part of Yunnan added a third genus of the group to the fern flora of this country. This note-worthy addition is represented by *C. assamica* (*Kaulfussia assamica* Griff.) Ching, comb. nov. previously known only from Assam, Northern India, but erroneously considered in the past as being identical with the Malaysian *C. aesculifolia* (Bl.) Maxon, from which the species from the Asiatic mainland differs in many respects.

In the present paper, we are primarily concerned with the genus *Archangiopteris*, which up to now was yet imperfectly understood as regards its origin, morphology, taxonomy and geographical distribution.

As far as the fossil remains go, it seems beyond doubt that the prototype of *Archangiopteris* dates back to the time of Coal Measures, typified by a fossil plant known as *Danacopsis fecunda* Halle from the Rhaetic coal mines of Billeholm, which, in spite of the implications of its name, conforms very closely to the genus *Archangiopteris* in the lanceolate pinnae and the long linear superficial sori consisting of two close rows of separate sporangia each dehiscing down by a ventral longitudinal slit, differing only in dichotomous lateral veins with reticulated intermediate veinlets, a condition perhaps due to the broadening of the webbing.

Phylogenetically, *Archangiopteris* represents the topmost twig of one of the evolutionary lines of the ancient Marratiaceous type of ferns, and its relation with *Angiopteris* is so close that it may with good reasons be considered as a direct descendant, although in the course of evolution through great geologic ages, acquired a series of characters significant enough to warrant its segregation as a distinct though closely related genus.

Geographically, this peculiar genus has now a restricted distribution, being confined to a rather narrow strip of earth surface of a mountainous nature, between 19–24° N. Lat. and 106–122° E. Long., where still exists a remnant of a more or less luxuriant tropical monsoon forest, in which the genus *Angiopteris* also flourishes as well as *Christensenia assamica* (Griff.) Ching of the same group discovered there two years ago for the first time in China. Considering the number of species now known, it may be safely inferred that the southeastern Yunnan-Tonkin region might be the original home of *Archangiopteris*. This area, characterized by comparatively stable tropical climatic conditions in the historic past coupled with complicated land features, seems to be a centre of distribution for many descendants and survivors of ancient tropical elements, some of which seem to have continued to develop into new forms as exemplified by *Archangiopteris* among the Filicales (Fig. 1, p. 202).

The genus *Archangiopteris* of the family *Angiopteridaceae* Carl Christensen, once placed in Marratiaceae by all other authors, ever since its founding by Christ and Giesenhagen in 1899, has been a subject of much morphological and phylogenetical interest, but remained imperfectly known owing to the scarcity of fresh material available for study. Since then four additional species—three from Indo-China on the Chinese borderland, another from Taiwan—have been ascribed to this what had been previously considered a monotypic genus. However, among collections made by

Chinese botanists during the last twenty years in southeastern Yunnan and on the Island of Hainan, five more species have been recognized, bringing the total number of species now known in the genus up to ten, at the same time, extending its geographical range from southeastern Yunnan through the southern part of Kwangsi Province to the Islands of Hainan and Taiwan. In this connection, it may be pointed out that the chief significance of these new discoveries lies not so much in the number of species increased, as in the revelation of an array of new characters of morphological and taxonomical importance, which combined contribute materially to a far better understanding of the genus as a whole. Among the new characters brought to light by my recent study, mention may be made of the following:

1) One of the diagnostic characters heretofore ascribed to *Archangiopteris* has been the "simply pinnate frond", by which the genus is distinguished from *Angiopteris*, as has been generally reiterated in current botanical literature. But since the discovery of a bipinnate-leaved species, *Archangiopteris bipinnata* Ching from southeastern Yunnan, this character no longer holds good, although simply pinnate fronds still remain to be a predominant feature of the genus.

2) It has long been known that the sori of *Archangiopteris* are usually provided with paraphyses called "fringed scales", or "false indusium" by authors in the past. However, the result of my study makes it evident that the paraphyses under the linear sori in *Archangiopteris* are not scales at all but really hairs, and their presence in the genus is not only constant but also affords a reliable character in specific diagnosis. The paraphyses consist of rod-like or cylindrical multicellular articulated hairs of varying length, sometimes more or less glandular at the apex, always freely branched from close to or above the base, and varying in length with different species. In most species they are usually as long as the sporangia, but in others, for example, *A. caudata* Ching from southern Kwangsi, they are so short as to be completely hidden underneath the sori, so that when seen from above, the sori appear as if exparaphysate (without paraphyses), while in another species, *A. hokouensis* Ching from Hokou, Yunnan, the paraphyses are decidedly longer than the sporangia, composed of up to 15 cylindrical septate cells, so densely crowded along the soriferous veins that the young developing sori virtually appear to push their way upwards from underneath the thick coating of long shaggy hairs.

3) The stipe of *Archangiopteris*, like that of *Danaea*, has been noted as being always provided with a single geniculated fleshy nodose swelling some distance above its base, or rather below its middle; and this is generally true of all the previously known species, but in the newly discovered *A. hokouensis* Ching, 4—5 such nodose swellings all spaced at fairly regular intervals occur along the entire length of the stipe, so that it looks somewhat like a bamboo culm in general appearance. It has been pointed out (Тахтаджян, Высшие растения I. 184, 1956.) that the characteristic nodose swelling on the stipe or petiole, actually an air-inflated joint full of sappy substance, is of considerable physiological significance in the life of modern Marrattiaceous ferns in as much as it is supposed to, as it actually does, serve as an effective mechanism for controlling the orientation of leaves in relation to the direction and intensity of sunrays falling upon them.

4) Another outstanding character distinguishing *Archangiopteris* from *Angiopteris* is the very long linear superficial sori which are composed of usually 40—60, sometimes up to 160 sporangia, medially situated along the veins. However, in the new species, *A. hokouensis* Ching, the sori measure up to 3—3.5 cm in length and consist of up to 240 sporangia.

5) In the past, The so-called spurious "recurrent veinlets" running downwards from the margin between each pair of true veins were not known to exist in *Archangiopteris*, but in *A. Cadieri* Tard. et C. Chr., a species discovered not long ago in Annam, the presence of "recurrent

veinlets" do occur. Moreover, in this species the rather short (3—4 mm) linear sori with 35—50 sporangia occupy a position nearer to the leaf-margin than to the costa of the pinnae very much in the same manner as in some species of *Angiopteris*. These two characters may be considered as additional evidence to support the view that *Archangiopteris* is a direct derivative from *Angiopteris*.

In spite of the fact that many important new characters of morphological significance have been revealed by the recent study of ample material in hand, through which some of the previously accepted distinctions between *Angiopteris* and *Archangiopteris* seem to have been greatly weakened, if not altogether broken down, the distinction between the two closely related genera still remains real and unmitakable, substantiated as it is by other new characters of even greater significance. In order to clarify the prevailing but quite misleading conception of the genus under review, a revision of the generic diagnosis and revaluation of the distinctions between *Archangiopteris* and *Angiopteris*, as far as our present knowledge goes, seem much to be desired.

**Archangiopteris** Christ et Gies. in *Flora* 86: 72—85, 1899; Diels in *Engl. u. Prantl, Nat. Pflanzenfam.* 1: iv. 439, 1899; C. Chr. *Ind. Fil.* 62, 1905; *Suppl.* III. 26, 1936; Tard. et C. Chr. in *Lecomte, Not. Syst.* 5: 5, 1935; in *Fl. Gen. Indo-chine* 7: 14, 1939; *Cop. Gen. Fil.* 15, 1947.

*Protomarrattia* Hayata in *Bot. Gaz.* 67: 88, fig. 1, 1919.

*Protangiopteris* Hayata in *Bot. Mag. Tokio* 42: 308, 1928.

Medium-sized terrestrial ferns inhabiting tropical mountain forests of evergreen broad-leaved trees. *Rhizome* rather elongate, suberect or oblique, dorsiventral with a few long unbranched incrassate fleshy roots; *fronds* fasciculate, several together, stipe long, rather slender, fleshy-herbaceous, broadly grooved above throughout the rachis, copiously clothed especially in the lower part in long, linear, coarsely dentate, dark brown, clathrate and peltately affixed thin scales and provided at the base with a pair of quite large fleshy, ovate-oblong persistent stipular appendages and upward with one or sometimes 4—5 geniculate fleshy nodose swellings which become collapsed and blackish upon drying; lamina ovate to deltoid, shorter than stipe. As a rule, simply impari-pinnate, or rarely bipinnate, generally with 1—6 pairs of alternate or subopposite, broadly lanceolate, acuminate, petiolate *pinnae* below a similar but usually larger free terminal pinna, petioles also inflated and turning blackish when dry; *venation* free, veins obliquely patent from the costa, once-forked above the base, or simple, distinct, extending from the costa to near the leaf margin with more or less antrorsely curved and attenuate apice, as a rule, without spurlous recurent veinlets (except in *A. Cadierei*); *texture* herbaceous or chartaceous, green, glabrous above, rachis and underside usually sparsely scaly; *sori* linear-elongate, dorsal on the veins, as a rule situated midway between the costa and margin, leaving a broad sterile space on each side of costa and along the margin, consisting of a great number (20—60—160—240) of boat-shaped free sessile sporangia having rudimentary annulus at the apice in two opposite close rows, opening down the ventral side by a longitudinal slit, and provided underneath with numerous, long or short, articulate, subglandular, translucent and branched hair-like paraphyses, easily abraded upon drying; *spores* roundish to broadly ovoid, yellowish-white, translucent with dense, short, fine echinoses (exospores).

A natural genus of about 10 species in Yunnan-Tonkin border extending from Southwest China eastwards to the southern part of Kwangsi and the islands of Hainan and Taiwan.

Without doubt, the genus is closely related to *Angiopteris*, from which it is technically distinguished by much smaller, simpler and slender habit having rather elongate, suberect dorsiventral rhizome with thin-fleshy ovate-oblong bivalved persistent stipules at the base of the slender stipe, which is always provided at about 20 cm or higher up above the base with one, or sometimes more, fleshy nodose swellings turning blackish upon drying; by the presence especially in the

lower part of the stipe of rather copious, linear-elongate, clathrate, coarsely dentate and peltately affixed scales; by the much smaller and simpler lamina, which, as a rule, is simply impari-pinnate (rarely bipinnate) with a few pairs of much larger and broadly lanceolate pinnae each provided with a fairly long and inflated petiole; by longer linear sori consisting of more numerous sporangia (generally 40—240), not inframarginal but situated midway between the costa and margin and provided underneath with numerous, articulate and freely branched hair-like paraphyses, and finally by finely echinose spores.

After the recognition of the genus *Archangiopteris* by Christ and Giesenhagen in 1899, then known only from the southeastern corner of Yunnan Province, China, the generic concept was greatly confounded by Hayata, who in a period of some ten years proposed two new genera, namely, *Protomarrattia* and *Protangiopteris* based upon specimens from Tonkin and Taiwan. While establishing the genus *Protangiopteris*, apparently without an intimate knowledge of *Archangiopteris* Christ et Gies., Hayata designated, as the basis of his new genus, what he thought to be three distinctive characters, namely, the presence of an inflated articulation below the middle of the stipe, the non-inflated petiole of the pinnae and the presence of numerous "scales" as false indusia underneath the sori, but, as we know now, these three characters are exactly some of the chief diagnostic distinctions of *Archangiopteris* from *Angiopteris* and, therefore, his genus must be regarded as a synonym of *Archangiopteris* Christ et Gies.

The same is also true of *Protomarrattia* Hayata. The genus, though accepted as valid by F. O. Bower (The Ferns Vol. II, p. 127), was based upon specimens from Tonkin with the young developing sori so crushed upon drying that they appeared to be composed of coherent sporangia (syngangium) as in *Marrattia*, otherwise his *Protomarrattia tonkinensis*, type of the genus, differs in no respect from *Archangiopteris tamdaoensis* Hayata from the same region, as has already been pointed out by Christensen and Tardieu-Blot (Lecomte, Not. Syst. 5: p. 3, 1935).

As was already commented upon by Bower (l. c. p. 122), the names of *Archangiopteris*, *Protomarrattia* and *Protangiopteris* are very misleading in their implications. For in the mind of their authors, these genera are supposed to be more primitive than both *Angiopteris* and *Marrattia*. But these assumed primitive ferns actually have sori more extended down the margin of pinnae than those of the older genera and bear scales on stipe and other parts instead of hairs, which both have generally been considered as some of the indications of primitiveness in ferns. A comparison with early fossils such as the Upper Devonian *Coenopteridaceae*, where the sori are rosette-like and marginal, clearly indicates these genera are no older than *Angiopteris* at all, but rather its derivatives.

Authors in the past have long been divided in their opinions as to whether the modern Marratiales should be represented by a single family *Marratiaceae*, or else be divided into several families or subfamilies. Carl Christensen (in Verdoorn, Manual of Pteridology pp. 527, 528-1938) was the first to propose, and I think appropriate, to divide the order into two families, namely *Angiopteridaceae* and *Marratiaceae*, on the chief ground that the former has sori consisting of free sporangia which are provided with rudimentary annulus at the apice, while the latter has syngangial sori of coalescent sporangia not crowned by a rudimentary annulus. On the other hand, Copeland (Gen. Fil. p. 14, 1947) thought this is not warranted on phylogenetical grounds, and he divided the order into four subfamilies, namely, *Angiopterideae*, *Marratiaceae*, *Kaulfussiae* and *Danaciae*, a disposition not compatible with evidences now available.

Early in 1940 I actually proposed to segregate the genus *Christensenia* as a family, *Christenseniaceae* (Bull. Fan Mem. Inst. Biol. Bot. Ser. 10: p. 227, 1940) for the chief reason that it

has dorsiventral rhizome with digitate fronds, reticulate venation and circular synangia with a hollow in the centre but without paraphyses. The results of ontogenetic studies also confirmed this decision, since the first young sporophytic leaf of *Christensenia* is spade-like in outline characterized by reticulate venation, while that of *Angiopteris*, *Danaea*, or *Marrattia* is fan-shaped with typically dichotomous free venation. This may also serve as a evidence, which tends to support the general belief that *Christensenia* is of a late descent in evolution as compared with other related genera. At about the same time, Campbell (Evolution of Land Plants p. 333, 1940) also suggested the segregation of *Christensenia* into a distinct family (*Kaulfussiaceae*).

I am still strongly of the opinion as I was long ago, that *Danaea* should likewise be separated from *Marratiaceae* into an independent family, *Danaeaceae* Agardh (Aphorismi Bot. p. 117. 1822, pro parte), thus leaving the genus *Marrattia* in a family of its own, for phylogenetically these two families represent distinct lines of evolution, although originated in all probability about the same geological time.

Summing up the above stated, it seems quite logical to divide the old comprehensive but very incongruent family *Marratiaceae* into four natural families, as follows:

1. **Angiopteridaceae** C. Chr. including three genera, *Macroglossum* Copel. *Angiopteris* Hoffm. and *Archangiopteris* Christ et Gies.

2. **Marratiaceae** Kaulf. with a single genus, *Marrattia* Swartz.

3. **Danaeaceae** Agardh with a single genus, *Danaea* Smith.

4. **Christensiaceae** Ching with a single genus, *Christensenia* Maxon.

Ample fossil remains seems to suggest that the cohesion of sporangia to form synangia was not necessarily a secondary modification derived from the ferns with free sporangial sori as was thought by Bower, but, as pointed out by Scott (Study of Fossil Botany I. p. 366. 1921), may have been originated in certain groups at very early period; and this is what actually took place, for even in Palaeozoic Times, ferns both with free sporangial sori as seen in *Scolecopteris*, *Eoangiopteris* and those with synangia of various forms represented by such tree-like ferns as *Ptychocarpus* and *Asterotheca* have been found in contemporaneous existence. Nor do I agree with Bower (The Ferns II. p. 110. 1927), who considered the circular type of synangia as exhibited by *Christensenia* is a result of modification by fission of linear type of sori, but, on the contrary, I am of the opinion that the fusion of isolated sori into coenosori seems to be the general course of evolution among ferns; and this is particularly apparent in some of the advanced groups of Leptosporangiate Ferns, while fission of sori in these ferns may be considered as a casual or abnormal rather than a general phenomenon. Furthermore, the similarity of a certain organ in different groups of organisms, as is well known, may often really be the result of convergent development and not necessarily an indication of phylogenetic relationships. This is particularly true of such characters in ferns at large, as soral conditions and the presence or absence of indusia in the sori, which were taken by elder pteridologists such as Hooker and Baker over half century ago to be basic criteria for classification of ferns. In this connection, it may be inferred, that the phyletic affinity of *Christensenia* may be traced back to such ancestral types as *Ptychocarpus*, or *Asterotheca* of Carboniferous Period with rosette-like synangia rather than to *Marrattia* of modern times, which has linear synangia, besides some other important morphological differences.

### **Key to the Species of *Archangiopteris***

1. Fronds bipinnate in the lower part, pinnae 10—12 pairs, 15 cm long, 2.5 cm broad,

- dentate ..... 1. *A. bipinnate*
1. Fronds always simply pinnate with much larger and fewer (1—7 pairs) pinnae.
  2. Pinnae with one spurious recurrent veinlet running from the margin downward between each pair of true veins; sori short (5—8 mm), situated much nearer to the margin of the pinnae than to the costa, with the sterile space on each side of costa broader than that along the margin ..... 2. *A. Cadieri*
  2. Pinnae devoid of spurious recurrent veinlets as above, sori much longer, situated midway between the margin and costa, with the sterile space along the costa almost equal to that along the margin.
  3. Stipe with 4 or 5 fleshy nodose swellings above the base; underside of pinnae moderately hairy, sori 3—3.5 cm long, densely paraphysate with long shaggy hairs ..... 3. *A. hokouensis*.
  3. Stipe with only one fleshy nodose swelling below the middle; underside of pinnae glabrous or without similar hairs, sori generally much shorter, paraphyses usually not so dense and shorter.
  4. Lateral pinnae falcately linear-lanceolate, the basal pair about half as long as those next above, all with broad and rounded, or subrounded base; margin entire ..... 4. *A. subrotundata*
  4. Lateral pinnae generally lanceolate, the basal pair as long as, or somewhat shorter than those next above, gradually narrowed towards the cuneate base.
  5. Pinnae opposite or subopposite, coarsely dentate-serrate along the margin; paraphyses much shorter than and hidden by the sporangia.
  6. Pinnae broadly oblanceolate with caudate apice, dentate along the margin from the base upward; paraphyses very short ..... 5. *A. cuadata*
  6. Pinnae ovate-lanceolate with acuminate apice, rather arcuately serrate along the margin from the base upwards; paraphyses longer ..... 6. *A. tonkinensis*
  5. Pinnae alternate, with entire, or at most undulate, or crenato-undulate margin; paraphyses as long as, or longer than sporangia.
  6. Pinnae broadly ovate-lanceolate, shortly acuminate towards the apice ..... 7. *A. latipinna*
  6. Pinnae lanceolate or oblanceolate, gradually longacuminate towards apice.
  7. Pinnae lanceolate, margin plane, entire or dentate-undulate, texture herbaceous; species from S. E. Yunnan and Tonkin.
  8. Pinnae 2—4 pairs with gradually acuminate apice; base symmetrical; sori 1—2 cm long ..... 8. *A. Henryi*
  8. Pinnae 5—7 pairs with abruptly caudate apice, base oblique; sori 1 cm long ..... 9. *A. subintegra*.
  7. Pinnae narrowly oblanceolate, margin undulate-crenate, repand, texture chartaceous, species from Taiwan ..... 10. *A. Somai*

**1. *Archangiopteris bipinnata*** Ching, Ic. Fil. Sin. 5: t. 203. 1958.

Pl. XLIX, 1.

Stipe 60—70 cm long, about 4 mm across, deeply grooved above, pale green, herbaceous, sparsely

clothed in the lower part in dark brown, lanceolate, acuminate appressed scales and provided with one nodose swelling at about 20—34 cm above the base; *lamina* deltoid-ovate, 40—50 cm long, about 22 cm broad at the middle, bipinnate at base, simply impari-pinnate upward; *pinnæ* 10—12 pairs, the basal 3—4 much the largest, about 5 cm apart, oblique, alternate, petiolate; basal pinnæ 16—19 cm long, 6—7 cm broad, on petioles 2.5—3 cm long, pinnate with 2—7 pairs of small, broadlanceolate, acuminate, sessile, patent, coarsely dentate lateral *pinnules* 2—3 cm long, below 1 cm broad above the round-cuneate base, terminal pinnule large, 7—10 cm long, to 2.8 cm broad; the upper simple pinnæ on petioles 4—6 mm long, linear-lanceolate, gradually long-acuminate, 17—12 cm long, 2—2.8 cm broad near the middle, base round-cuneate, margin from base to apex regularly and prominently dentate; rachis compressed when dry, very narrowly winged on each side towards the apex; *veins* distinct on both sides, about 2 mm apart, generally simple or forked from above the base, diverging almost at a right angle to the costa and run straight towards the margin into each tooth; *texture* herbaceous, drying green, glabrous except for a few small brown scales on the costa beneath and also on the inflated petiole; *sori* linear, straight, to about 5 mm long, extending from near the costa to 4 mm within the leaf-margin, simple, or forked along the forked veins, each consisting of about 20—40 sporangia with dense brown, branched paraphyses underneath and as long as the sporangia; sori on the pinnules of the lower pinnæ shorter, of about 10—12 sporangia, starting from the costule but fall short of the leaf-margin; *spores* pale-colored, translucent, round but angular with verrucose surface.

Southeast Yunnan: Markuan Hsien, Ching-kou (Lao Ching Shan), K. M. Feng 13679, December 7th, 1947, in mixed forest, rare, 1100—1300 m. alt.

One of the most distinct species in the genus, resembling *Marrattia* in general habit. It can easily be distinguished from all the species known up to now by more memorous, much narrower and prominently dentate pinnæ, of which the lower 3—4 are again pinnate, by the straight, patent and generally simple veins, as well as by much shorter sori starting from near the costa and extending outwards to within 4 mm of the leaf-margin.

**2. *Archangiopteris Cadieri*** Tard. et C. Chr. in Lecomte, Not. Syst. 5: 8, pl. 1. fig. 1—2. 1936; in Fl. Gen. Indo-Chine 7: 15. 1939.

Annam: Cua Tung, *Cadiere* san no. (type), Mars-Avril, 1932, 50—100 m. altitude.

This Annamite species from a rather low elevation differs from all others of the genus in the presence of spurious recurrent veinlets about 1 cm long each starting from the margin of pinnæ downward between each pair of true veins, much in the manner of some species in *Angiopteris*, a character not known before in *Archangiopteris*. Another quite unique character of the species is the rather short sori, composed of about 35—50 sporangia, which extends outwardly to a short distance from the leaf-margin and inwardly leave a broad sterile space along each side of the costa, thus imparting to the plant a superficial resemblance to species of *Angiopteris*, which have a rather broad sterile area along the margin of the pinnæ. Consequently, in several respects, the species seems to be an intermediate link between the two phylogenetically closely related genera, *Archangiopteris* and *Angiopteris*.

**3. *Archangiopteris hokouensis*** Ching, Ic. Fil. Sin. 5: t. 204. 1958. Pl. XLIX, 2.

*Rhizome* thick, suberect, 3—4 cm across, roots thickened, carnose, terete, blackish, simple, growing abundantly out from the under side of rhizome; *fronds* fasciculate, stipe to 50 cm long, 5 mm across, fleshy-herbaceous, green, provided above the base and throughout its entire length with 4—5 equally spaced nodose swellings in the appearance of a bamboocane and also copiously with dark-brown ovate-lanceolate scales having a cordate base; *lamina* broadly ovate, to 30 cm long,

38 cm broad, imparipinnate; lateral *pinnae* 2—3 pairs, subopposite or alternate, about 4 cm apart, 15—20 cm long, 5—7 cm broad, elliptic-lanceolate, petiolate (petiole about 1.5 cm long, swollen, scaly and dry blackish), apex caudate-acuminate and coarsely serrate, narrowed towards cuneate base, margin coarsely arcuate-serrate, or crenate-dentate, the terminal pinna similar to the lateral ones but larger, 20—22 cm long, 7—9 cm broad; *veins* suberect-patent, conspicuous, generally forked, or rarely simple, upcurved towards the margin and extending into the teeth; *texture* chartaceous, dark green above and pale green beneath, with moderately scattered short and articulate hairs; *sori* linear, 3—3.5 cm long or longer, separated by interstitial space as broad, consisting of 160—240, 2-rowed sporangia, the sterile space along both the margin and the costa about 5 mm broad, *paraphyses* very dense, filiform, branched, articulate, 10—15-celled, much longer than the sporangia, *spores* roundish or oblong, densely and minutely echinose.

Southeast Yunnan: Hokou, Nan-chi, *Chu Ve-ming* 1726, July 1955, in densely wooded moist ravine, 150 m. alt.

A remarkable species, differing from all other known species of the genus in having 4 or 5 nodose swellings above the base of the fleshy stipe, unusually broad elliptico-lanceolate serrate pinnae densely glandular hairy on the under surface, very long sori which extend from near the costa outwards to a short distance from the margin, and particularly in very long dense, branched shaggy paraphysate hairs almost completely covering the young developing sori.

#### 4. *Archangiopteris subrotundata* Ching, Ic. Fil. Sin. 5: t. 206. 1958. Pl. L, 1.

*Stipe* 36—60 cm long, greenish, deeply grooved on the upper side, with one nodose swelling 20—30 cm above the base, copiously clothed especially in the lower part in reddish brown linear scales; *lamina* about 40 cm long and as broad, broadly ovate, simply impari-pinnate; *pinnae* 4—5-jugate below the similar terminal pinna, alternate, about 4 cm apart, petiolate (petiole 7 mm long, inflated), the basal pair much shortened (14 cm long) and like those next above rather strongly falcate, base rounded, the upper ones 22—25 cm long, to 5 cm broad at the middle, broadly linear-lanceolate, gradually acuminate, base rounded or subrounded, not cuneate, margin entire or at most slightly wavy below the dentate-serrate apical part; *texture* thin herbaceous, green, glabrous excepting on the sparsely scaly costa beneath; *veins* patent, distinct beneath, 4 mm apart, forked or simple, decidedly curved upward towards the margin; *sori* linear, generally 8—12 mm long, far apart, situated midway between the costa and margin, leaving an equally broad sterile space on each side, densely paraphysate with freely branched articulate hairs longer than the sporangia; *spores* oblong-reniform, finely echinose.

Southeast Yunnan: Si-chour Hsien, Faadoon, *K. M. Feng* 12019, Sept. 21th. 1947, in mixed forest, 1500—1600 m. alt.

Closely related to *A. Henryi* Christ et Gies. from the same region, but differs in the decidedly falcate lateral pinnae, of which the basal pair is only about half as long as those next above, in the broadly linear-lanceolate pinnae hardly narrowed towards the rounded or subrounded base, with entire or at most slightly wavy margin.

#### 5. *Archangiopteris caudata* Ching, Ic. Fil. Sin. 5: t. 208. 1958. Pl. L, 2.

*Rhizome* suberect, about 2 cm across, roots long, thickened, carnose, unbranched, growing rather abundantly from the under side of rhizome, *fronds* solitary (according to the type), *stipe* 30—45 cm long, 3—4 mm across, green, subglabrous with a nodose swelling and geniculate about 16 cm above the base; *lamina* ovate, 30 cm long, about 25 cm broad, impari-pinnate; *pinnae* 2 pairs, subopposite, 5—6 cm apart, of similar size, 18 cm long, 4.5—5 cm broad at the middle,



broadly oblanceolate, gradually narrowed towards cuneate base, apex suddenly caudate (cauda 1.5 cm long, linear, serrate), margin from the base upward coarsely dentate, the endpinna similar to the lateral ones but slightly larger; *texture* herbaceous-chartaceous, green, both sides glabrous; *veins* suberect-patent, running from the costa outward under an angle of about 60°, mostly forked or sometimes simple, upcurved towards the margin and extending into the teeth; *sori* linear, 8—10 mm long, falling short about 6 mm from both the margin and the costa, subcontiguous, each consisting of about 40—70, or rarely more sporangia, receptacle slightly elevated, *paraphyses* rather sparse, reddish-brown, articulate, much shorter than the sporangia and branched profusely from the base; *spores* globose-tetraedric, densely and minutely echinose.

Southern Kwangsi: Min River, Kang Nu Shan, specimens ex Herb. Kwangsi University, in ravine under the forest, about halfway up the mountain, October 2, 1935.

A very distinct species, differing from *A. Henryi* Christ et Gies. in oblanceolate pinnae with abruptly caudate apice, coarsely dentate leaf-margin, and in the very short and profusely branched paraphyses so completely hidden under the sori that their presence can hardly be detected from above.

## 6. *Archangiopteris tonkinensis* (Hayata) Ching, Ic. Fil. Sin. 5: t. 209. 1958.

Pl. LI, 1.

*Protomarrattia tonkinensis* Hayata in Bot. Gaz. 67: 88, fig. 1. 1919.

*Archangiopteris tamdaoensis* Hayata in Bot. Gaz. 67: 90, fig. 2. 1919; C. Chr. Ind. Fil. Suppl. III. 26, 1933; C. Chr. et Tard. in Lecomte, Not. Syst. 5: 5. 1935; in Fl. Gen. Indochine. 7: 17. 1939.

*Protaniopteris tamdaiensis* Hayata in Bot. Mag. Tokio 42: 309, 1928.

Hainan: Five Finger Mount., Shan Ah Ping, C. L. Tso 44148, October 24, 1932, in woods, 3000 ft. alt.; southern slope of the same locality, F. A. McClure 9470, May 19, 1922, in wooded ravine; C. Wang 35723, December 20, 1933, by stream side.

Tonkin: Tamdao, B. Hayata (type), Août, 1917; Pételot 3956, Mai, 1913; environs de Chapa, Pételot Août, 1913, vers 1300 m. alt.

Annam: Cua Tung, Cadière Mai, 1934.

*Stipe* 40—45 cm long, pale green, broadly grooved in its whole length above, scaly particularly near the base, with a nodose swelling at 20—30 cm above the base; *lamina* broadly obovate in outline, much shorter than stipe; *pinnae* 2—4 pairs, opposite, ovate-lanceolate, 20—25 cm long, 4—5 cm broad, petiolate (petiole about 5 mm long), gradually narrowed towards both ends, apex long-acuminate, base shortly cuneate, margin serrate with rather sharp arcuate teeth; *texture* more or less thickly chartaceous, glabrous above, very sparsely scaly beneath; *sori* 7—10 mm long, midway between the costa and margin, finely paraphysate with branched articulate hairs shorter than sporangia, finally becoming abraded; *spores* roundish-oblong, minutely and densely echinose.

The present species closely resembles *A. Henryi* Christ et Gies., differing in much longer stipes, which are about twice as long as the lamina, ovate-lanceolate, opposite pinnae with regularly and rather arcuately serrate margin, and in having paraphyses much shorter than the sporangia.

## 7. *Archangiopteris latipinna* Ching, Ic. Fil. Sin. 5: t. 207. 1958.

Pl. LI, 2.

*Stipe* 47—55 cm long, 5 mm across, deeply sulcate above, moderately scaly in the lower part, with one nodose swelling at about 20 cm above the base; *lamina* oblong-ovate, 35—45 cm long, 26—30 cm broad, imparipinnate; *pinnae* 2—3-jugate, alternate, 4—5 cm apart, oblique, the basal pair only slightly shorter than the next pair above, the lower ones falcately recurved, the upper

ones to 20 cm long, 5—5.5 cm broad in the broadest part near the middle, broadly ovate-lanceolate, gradually narrowed towards the cuneate base, apice rather short-acuminate and serrate, margin entire and more or less repandulate; petiole about 1 cm long, scarcely inflated, subglabrous; *texture* thickly chartaceous, both sides glabrous, pale green beneath; *veins* lax, patent, forked or simple, antrorsely curved towards the margin, distinct on both sides; *sori* 1—1.5 cm long, midway between the margin and costa, leaving a sterile space about 7 mm broad equally as wide along the margin as along the costa, and separated from each other by broader interstitial spaces; *paraphyses* quite dense, longer than the sporangia.

Southeast Yunnan: Ping-pien Hsien, H. T. Tsai 60299, June 19, 1934, in woods, 1200 m. alt.

For a long time I have considered the species the same as *A. Henryi* Christ et Gies. from the same region, from which, however, it really differs in the broadly ovate pinnae of a thickly chartaceous texture, of which the lower ones decidedly falcate, the rather short-acuminate apice, the repandulate leaf-margin, and the longer sori.

**8. *Archangiopteris Henryi*** Christ et Giesenhagen in Flora 86: 72—85. fig. 1—5, 1899; Christ in Bull. Herb. Boiss. 7: 14, 1899; Diels in Engl. u. Prantl: Nat. pflanzenfam. 1: 4. 439. 1899; C. Chr. Ind. Fil. 62, 1905; Hu et Ching, Ic. Fil. Sin. 1: t. 2, 1930; Cop. Gen. Fil. 15. 1947.

*Rhizome* suberect, about 2—3 cm across, fleshy, furnished with long naked thickened and fleshy roots, glabrous except the growing tips which are sparsely scaly; *fronds* fasciculate, stipe 40—60 cm long, or longer, about 2.5 mm across, broadly grooved throughout its whole length above, green, herbaceous, inflated slightly below the middle, copiously scaly especially towards the basal part with linear-lanceolate, fairly long, brown or dark-brown, thin, persistent *scales*; *lamina* as long as stipe, about 17 cm broad, ovate, simply pinnate; *pinnae* 2—4 pairs under the similar though often larger terminal pinna, which sometimes reaches to 30 cm long and 6.5 cm broad, alternate, oblique, about 5—6 cm apart, petiolate, the basal pair slightly shorter, 12—15 cm long, about 3 cm broad, the upper ones larger, 17—20 cm long, 4—5 cm broad in the broadest middle part, broad-lanceolate, gradually acuminate, base cuneate, gradually narrowed with the inflated, blackish and scaly petiole about 1 cm long. margin entire or slightly undulate, but acutely serrate towards apex; *veins* fine, lax, about 4 in 1 cm, very patent, distinct on both sides, mostly once forked, or often with simple and forked ones alternating, attenuate and upcurved at the apex ending a short distance within the margin; *texture* herbaceous, dry green, glabrous on both sides except the costa on the lower surface provided with a few brown, linear-lanceolate scales; *sori* linear, straight, 10—20 mm long, separated by spaces equally broad, consisting of 60—160 sporangia, situated midway between the costa and margin, densely paraphysate underneath with reddish, fine, articulated branched hairs longer than the sporangia.

Yunnan: Mengtze, mountains to the southeast, *A. Henry* 11544 (type), in forest, 5000 ft. alt.; Pin Pien Hsien, Ta Wei Shan K. M. Feng 4605, Sept. 21, 1954, in moist wooded ravine, 1100—1200 m. alt.; K. M. Feng 5078, under the moist forest, October 18, 1954; C. W. Wang 82370 (1939); Mar-li-po, Kwan Kao, on the border of Tonkin, C. W. Wang 86938, Feb. 16th, 1940, in densely wooded valley, 1200 m. alt.

The species is the type of the genus *Archangiopteris* now found to be fairly common under evergreen forests in Ta Wei Shan in the districts of Ping Pien and Hokou, Southeast Yunnan.

Its salient characters are the lanceolate and alternate pinnae gradually acuminate and serrate at the apex, gradually attenuated to a cuneate base, the entire or undulate or at most undulate

dentate along the margin, and the inflate and blackish scaly petiole which averages about 1 cm long. The paraphyses under the sori are rather dense and shaggy, of a brownish color, and longer than the sporangia.

**9. *Archangiopteris subintegra*** Hayata in Bot. Gaz. 67: 90, fig. 1. 1919; C. Chr. Ind. Fil. Suppl. III. 26. 1936; Tard. et C. Chr. in Lecomte, Not. Syst. 5: 5. 1935; in Fl. Gen. Indochine 7: 15. 1939.

Tonkin: entre Chapa et Muong Xen, on the Chinese border, *B. Hayata* (type), July 1917; entre Chapa et Ta Phinh, *Pételot*, Sept. 1932 m vers 1550 m. alt.

*Petiole* to 70 cm long, the basal part covered with scales which are lanceolate from a broad rounded base, marked by a single inflated articulation below the middle; *lamina* obovate, imparipinnate; *pinnæ* 5—7 pairs, lanceolate, petiolate (petiole 7 mm long, inflated and scaly), 20—25 cm long, 3—5 cm broad, abruptly contracted towards the apex into a linear acumen 2—3 cm long, base oblique, margin subentire or undulate, repand; *texture* thin; *sori* 1 cm long, equally distant from both the margin and the costa, thinly paraphysate; *spores* round, minutely echinose.

The species might well be regarded as a form of *A. Henryi* Christ et Gies. which has been already recorded from the same region.

**10. *Archangiopteris Somai*** Hayata, Ic. Pl. Form. 5: 256. 1915; 6: 154. fig. 60, Pl. 19. 1916; C. Chr. Ind. Fil. Suppl. I. 4. 1916; Suppl. III. 26. 1933; Nakai in Bot. Mag. Tokio 41: 78. 1927; M. Genkai, Short Fl. Form. 1. 1936; H. Ito, Fil. Jap. Illustr. Pl. 498. 1944; Ching, Ic. Fil. Sin. 5: t. 205. 1958. Pl. LII. *Angiopteris Somai* Hayata apud Makino et Nemoto, Fl. Jap. 1563. 1925.

*Protangiopteris Somai* Hayata in Bot. Mag. Tokio 42: 308. 1928.

Taiwan: Bahao, *T. Soma* (type), December 1910; Rengechi, Taichu, *S. Sasaki*, March 3, 1927; Yamamota & Mori, 2—3 Nov. 1932; Taihoku-syu, Bunzon-gun, Kanica, Y. Yamamota, July 24. 1938.

A fairly common fern in mountain forests in the southern, middle and northern parts of the island. *Stipe* 50—60 cm long, scaly in the lower part, with one nodose swelling at about 25 cm above the base; *petiole* 1 cm long; *pinnæ* 3—5, 20 cm long, 4 cm broad, oblanceolate, slightly narrowed from the middle downward into a rather broadly cuneate base, apex caudate-acuminate with a linear acumen 3—4 cm long; *veins* very patent, alternately forked and simple; margin repand, rather irregularly crenate-dentate above the base; *sori* linear, to 1.5 cm long, medial, leaving a broad sterile space on each side of costa and along the margin.

The Taiwan species, of which I have seen half a dozen specimens, is quite near *A. Henryi* Christ et Gies. from the mainland, and seems to differ in elongate oblanceolate pinnæ of a thicker texture with crenate-dentate and often repand margin.

### Principal References

- [1] Campbell. Eusporangiate Ferns, 1911.
- [2] Bower. The Ferns, Vol. II. 1926.
- [3] Ching: *Christenseniaceae*, A New Fern Family in Tropical Asia in Bull. Fan Mem. Inst. Biol. Bot. Ser. Vol. 10. p. 227. 1940.
- [4] Christensen. Index Filicum, 1905, Supplementum III. 1936.
- [5] Christensen. Filicinae in Verdoorn, Manual of Pteridology, 1938.
- [6] Christensen & Tardieu-Blot in Lecomte, Notulae Systematicae Vol. 5, Fougères D'Indochine, 1935.
- [7] Diels; Engler u. Prand, Naturlichen Pflanzenfamilien Band 1: 4. 1899.
- [8] Hayata. Icones Plantarum Formosarum Vols. 5. 1915 & 6. 1916.

- [9] Hirmaer, *Geographie und Zeitliche Verbreitung der Fossilen Pteridophyten* in Verdoorn, *Manual of Pteridology*, 1938.
- [10] Holttum, *Flora of Malaya*, Vol. II, Ferns, 1954.
- [11] Scott, *Studies of Fossil Botany*, Vol. I, 1921.
- [12] Tardieu-Blot & Christensen, *Flore Generale D'Indochine* Vol. 7, 1939.
- [13] Тахтаджян, *высшие растения*, I, 1956.
- [14] Wu and Wang (吴征镒, 王文采), 云南热带亚热带植物区系研究初步报告 (1). *植物分类学报* Vol. 6: 153—254 及 267—300.

## Explanation of Plates

### Plate XLIX, 1. *Archangiopteris bipinnata* Ching.

1. Habit sketch,  $\times \frac{1}{2}$ ;
2. Part of pinna, showing venation, serrature and sori,  $\times 1.5$ ;
3. Scale from the lower part of stipe,  $\times 15$ ;
4. Two sporangia attached to the vein with paraphyses,  $\times 15$ ;
5. Two sporangia detached, showing longitudinal slit on the ventral side,  $\times 7.5$ ;
6. Paraphysis detached from the sori,  $\times 37.5$ ;
7. Spores,  $\times 37.5$ .

### Plate XLIX, 2. *Archangiopteris hokouensis* Ching.

1. Habit sketch,  $\times \frac{1}{2}$ ;
2. Part of pinna, showing venation, serrature and sori, also hairy under surface,  $\times 1\frac{1}{2}$ ;
3. Scale from the lower part of stipe,  $\times 15$ ;
4. Two sporangia attached to the vein with paraphyses,  $\times 7.5$ ;
5. Two paraphyses removed from the sori,  $\times 22.5$ ;
6. Spores,  $\times 37.5$ , one enlarged,  $\times 150$ .

### Plate L, 1. *Archangiopteris subrotundata* Ching.

1. Habit sketch,  $\times \frac{1}{2}$ ;
2. Part of pinna, showing venation, leaf-margin and sori,  $\times 1.5$ ;
3. Scale from the lower part of stipe,  $\times 11.25$ ;
4. Two sporangia attached to the vein with paraphyses,  $\times 7.5$ ;
5. Two paraphyses removed from the sori,  $\times 37.5$ ;
6. Spores,  $\times 37.5$ , one enlarged  $\times 150$ .

### Plate L, 2. *Archangiopteris caudata* Ching.

1. Habit sketch,  $\times \frac{1}{2}$ ;
2. Part of pinna, showing venation, serrature and sori,  $\times 1.5$ ;
3. Scale from the lower part of stipe,  $\times 11.25$ ;
4. Two sporangia attached to the vein with short paraphyses,  $\times 7.5$ ;
5. Paraphyses removed from the sori,  $\times 37.5$ ;
6. Spores,  $\times 37.5$ , one enlarged,  $\times 150$ .

### Plate LI, 1. *Archangiopteris tonkinensis* (Hayata) Ching.

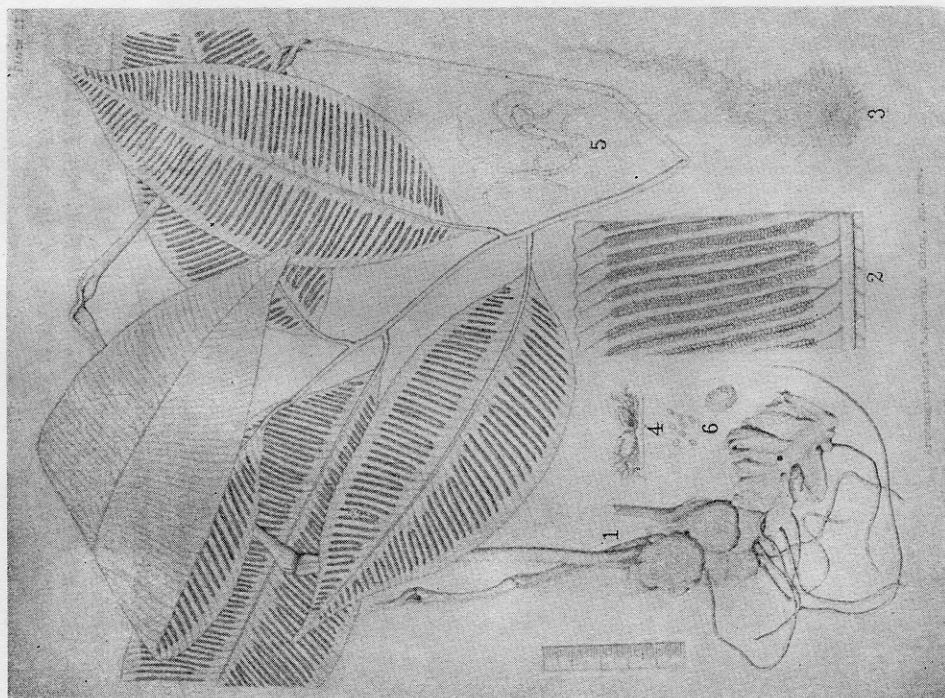
1. Habit sketch,  $\times \frac{1}{2}$ ;
2. Part of pinna, showing venation, serrature and sori,  $\times 1.5$ ;
3. Scale from the basal part of stipe,  $\times 11.25$ ;
4. Two sporangia attached to the vein with paraphyses,  $\times 7.5$ ;
5. Paraphyses removed from the sori,  $\times 37.5$ ;
6. Spores,  $\times 37.5$ , one enlarged,  $\times 150$ .

### Plate LI, 2. *Archangiopteris latipinna* Ching.

1. Habit sketch,  $\times \frac{1}{2}$ ;
2. Part of pinna, showing venation, leaf-margin and sori,  $\times 1.5$ ;
3. Scale from the lower part of stipe,  $\times 11.25$ ;
4. Two sporangia attached to the vein with paraphyses,  $\times 7.5$ ;
5. Paraphysis removed from the sori,  $\times 37.5$ ;
6. Spores,  $\times 37.5$ , one enlarged,  $\times 150$ .

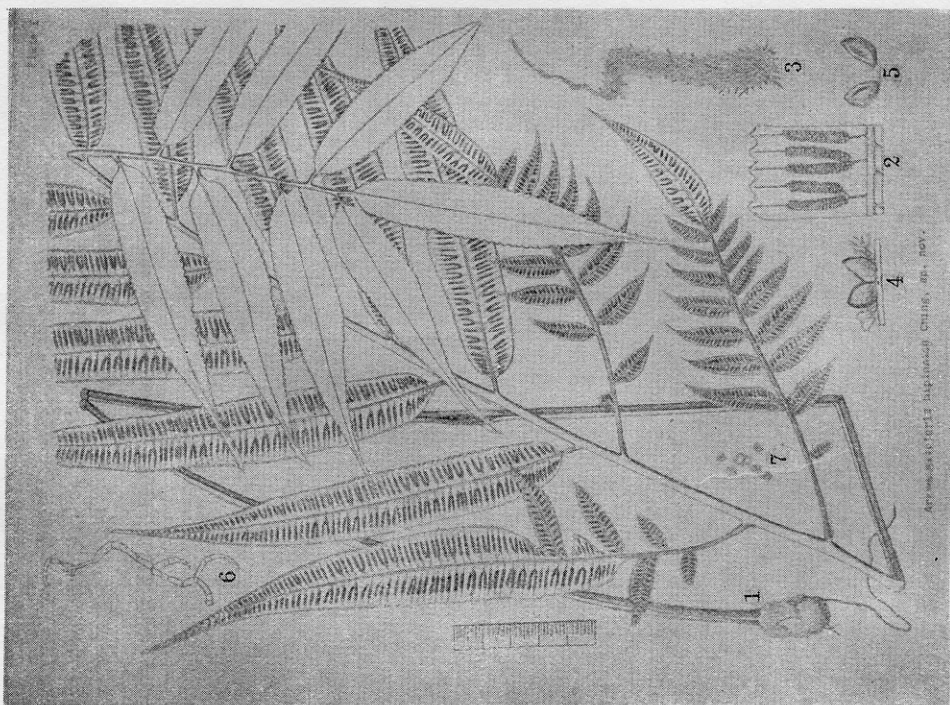
### Plate LII. *Archangiopteris Somai* Hayata.

1. Habit sketch,  $\times \frac{1}{2}$ ;
2. Lower part of pinna, showing venation, serrature and sori,  $\times 1.5$ ;
3. Scale from the lower part of stipe,  $\times 11.25$ ;
4. Cross section of the basal part of stipe,  $\times 1.5$ ;
5. Cross section of the middle part of stipe,  $\times 1.5$ ;
6. Cross section of the upper part of stipe,  $\times 1.5$ ;
7. Two sporangia attached to the vein with paraphyses,  $\times 7.5$ ;
8. Paraphyses removed from the sori,  $\times 37.5$ ;
9. Spores,  $\times 37.5$ , one enlarged,  $\times 150$ .



2. 河口原始观音座蓮 (*Archangiopteris hokouensis* Ching)

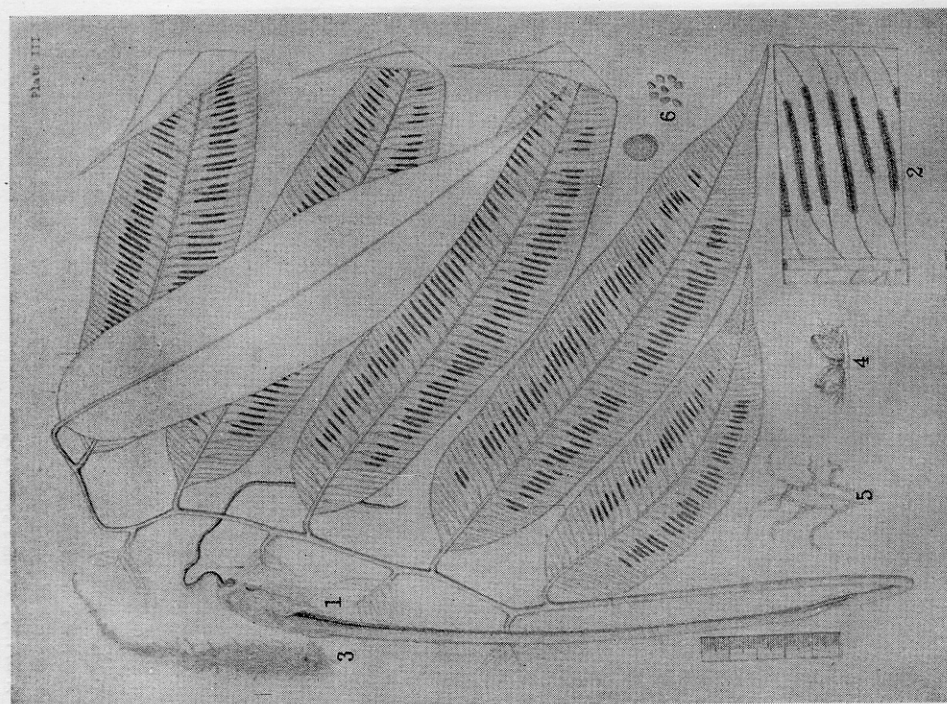
1. 本种全形,  $\times \frac{3}{8}$ ; 2. 羽片的一部分, 示叶脉、锯齿、子囊群和下面的腺毛,  $\times 1\frac{1}{2}$ ; 3. 叶柄下部的鳞片,  $\times 15$ ; 4. 两个着生于托上的子囊和夹丝,  $\times 7.5$ ; 5. 两根夹丝,  $\times 22.5$ ; 6. 孢子,  $\times 37.5$ , 另一个  $\times 150$ 。



1. 二回原始观音座蓮 (*Archangiopteris bipinnata* Ching)

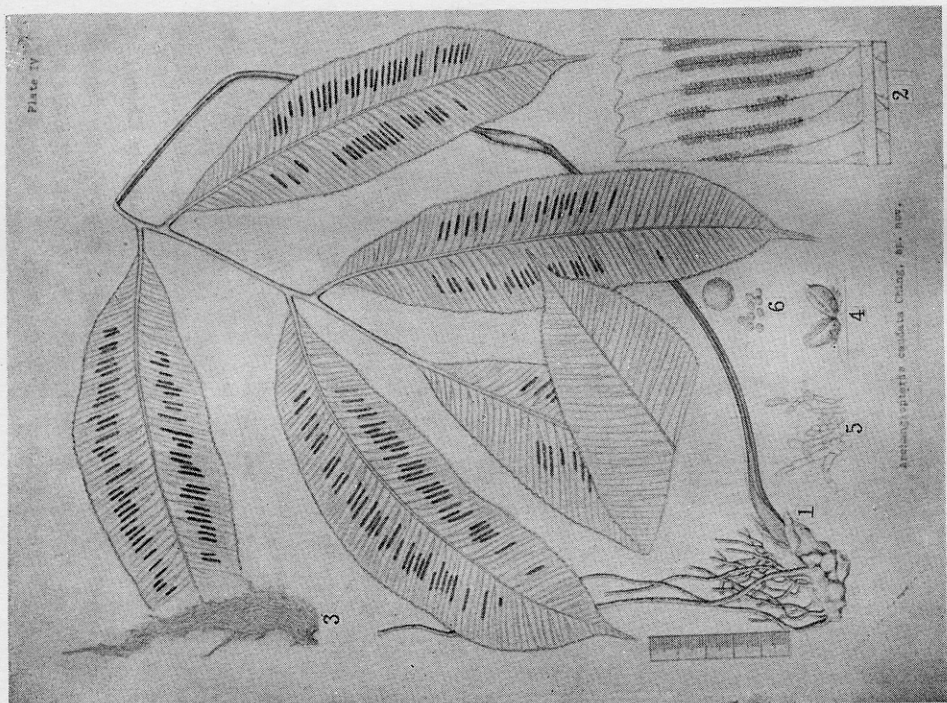
1. 本种全形,  $\times \frac{3}{8}$ ; 2. 一回羽片的一部分, 示叶脉与子囊群,  $\times 1\frac{1}{2}$ ; 3. 叶柄下部的鳞片,  $\times 15$ ; 4. 两个孢子囊着生于有夹毛的托上,  $\times 15$ ; 5. 两个分离的孢子囊, 示腹面的縱裂縫,  $\times 7.5$ ; 6. 子囊群下的夹毛,  $\times 37.5$ ; 7. 孢子,  $\times 37.5$ 。





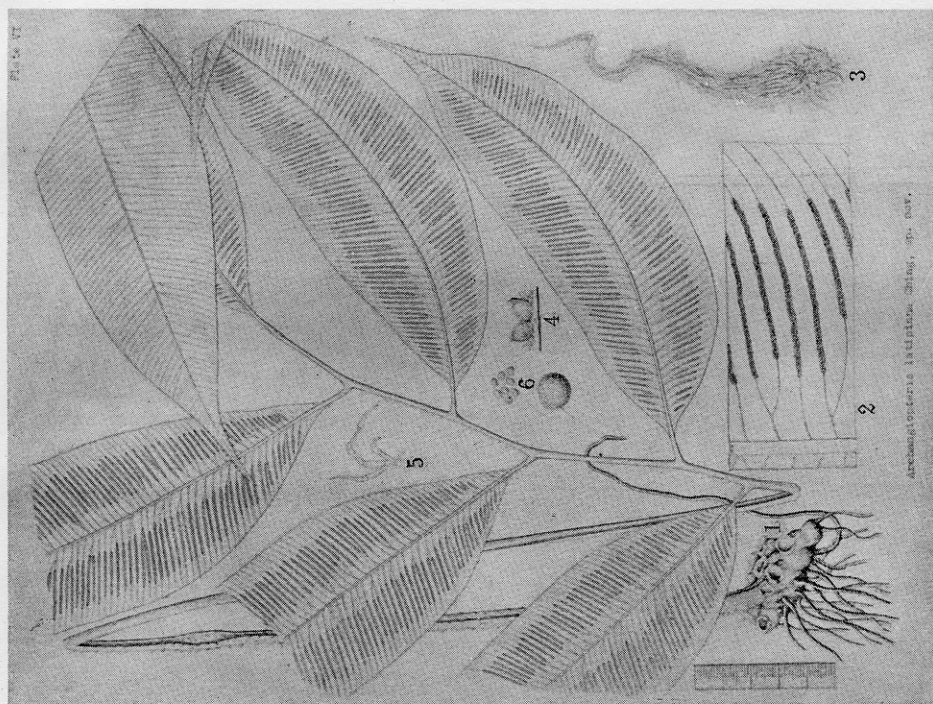
1. 圓基原始音座蓮 (*Archangiopteris subrotundata* Ching)

1. 本種全形,  $\times \%$ ; 2. 羽片的一部分, 示葉脈、葉緣和子囊羣,  $\times 1.5$ ;  
3. 葉柄下部的鱗片,  $\times 11.25$ ; 4. 兩個孢子囊着生于有夾絲的托上,  
 $\times 7.5$ ; 5. 二條夾絲,  $\times 37.5$ ; 6. 孢子,  $\times 37.5$ ; 另一個  $\times 150$ 。



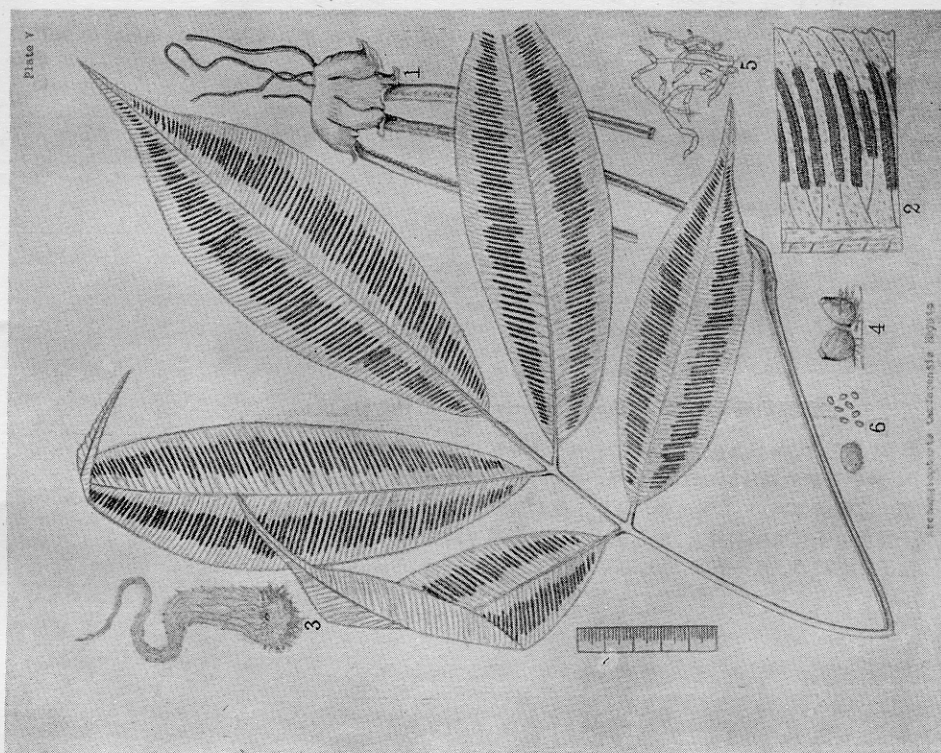
2. 尾葉原始音座蓮 (*Archangiopteris caudata* Ching)

1. 本種全形,  $\times \%$ ; 2. 羽片的一部分, 示葉脈、鋸齒及子囊羣,  $\times 1.5$ ;  
3. 葉柄下部的鱗片,  $\times 11.25$ ; 4. 子囊羣橫斷面, 示生于托上的二個  
子囊和短夾絲,  $\times 7.5$ ; 5. 夾絲,  $\times 37.5$ ; 6. 孢子,  $\times 37.5$ , 另一個  
 $\times 150$ 。



2. 潤葉原始觀音座蓮 (*Archangiopteris latipinna* Ching)

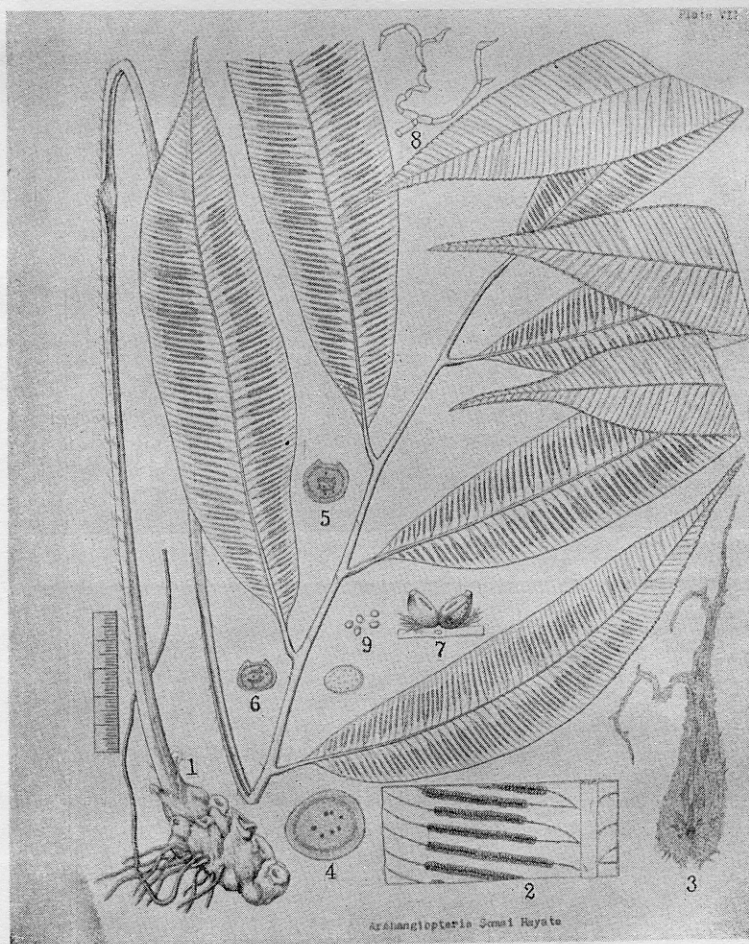
1. 本種全形,  $\times \frac{3}{8}$ ; 2. 羽片的一部分, 示葉脈、鋸齒和子囊羣,  $\times 1.5$ ;  
3. 葉柄下基的鱗片,  $\times 11.25$ ; 4. 兩個孢子囊着生于有夾絲的托上,  
 $\times 7.5$ ; 5. 子囊羣下的夾絲,  $\times 37.5$ ; 6. 孢子,  $\times 37.5$ , 另一個  $\times$   
150。



1. 尖葉原始觀音座蓮 (*Archangiopteris tonkinensis*  
(Hayata) Ching)

1. 本種全形,  $\times \frac{3}{8}$ ; 2. 羽片的一部分, 示葉脈、鋸齒和子囊羣,  $\times 1.5$ ;  
3. 葉柄基部的鱗片,  $\times 11.25$ ; 4. 兩個孢子囊着生于有夾絲的托上,  
 $\times 7.5$ ; 5. 子囊羣下的夾絲,  $\times 37.5$ ; 6. 孢子,  $\times 37.5$ , 另一個  $\times$   
150。





台灣原始觀音座蓮 (*Archangiopteris Somai* Hayata)

1. 本種全形,  $\times \frac{3}{8}$ ; 2. 羽片的一部分, 示葉脈, 鋸齒和子囊羣,  $\times 1.5$ ;
3. 葉柄下部的鱗片,  $\times 11.25$ ; 4. 葉柄下部的橫切面,  $\times 1.5$ ; 5. 葉柄中部的橫切面,  $\times 1.5$ ; 6. 葉柄上部的橫切面,  $\times 1.5$ ; 7. 兩個孢子囊着生于有夾絲的托上,  $\times 7.5$ ; 8. 子囊羣下的夾絲,  $\times 37.5$ ; 9. 孢子,  $\times 37.5$ , 另一個  $\times 150$ 。